Received: 10 March 2025 | Accepted: 5 December 2025

DOI: 10.1111/1365-2745.70261

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

RESEARCH ARTICLE

Climatic niche position determines post-fire resilience in Mediterranean forests

Gerard Codina[1,2] | Martina Sánchez-Pinillos[3] | Francisco Lloret[1,2] | Judit Lecina-Diaz[4] | Enric Batllori[5,6]

[1]Unitat d'Ecologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma Barcelona (UAB), Barcelona, Spain; [2]Centre de Reserca Ecologica i Aplicacions Forestals (CREAF), Barcelona, Spain; [3]Centre for Forest Research, Université du Québec à Montréal (UQAM), Montreal, Quebec, Canada; [4]TUM School of Life Sciences, Ecosystem Dynamics and Forest Management Group, Technical University of Munich, Freising, Germany; [5]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Barcelona, Spain and [6]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain

Correspondence
Gerard Codina
Email: g.codina@creaf.uab.cat

Funding information
European Union's Horizon 2020, Marie Skłodowska-Curie, Grant/Award Number: 891477; Ministerio de Ciencia, Innovación y Universidades, Gobierno de España, Grant/Award Number: PID2020-115264RB-I00; Natural Sciences and Engineering Research Council of Canada (DIVERSE project); Beca Impulsa CREAF-Barraquer; Generalitat de Catalunya Serra Húnter; Agència de Gestió d'Ajuts Universitaris i de Recerca, Grant/Award Number: 2021-SGR 00849

Handling Editor: Peter Vesk

Abstract

1. Fires are a common and significant disturbance in Mediterranean forest ecosystems with a prominent role in their dynamics. The increased frequency, intensity and extent of fires due to climate change are, however, expected to exceed forests' resilience capacity. It is still unknown how resilience capacity changes across species' biogeographical ranges in relation to pre- and post-fire environmental variability.
2. We analysed the resilience of Mediterranean pinewoods (*Pinus halepensis* and *P. nigra*) to fire in the Eastern Iberian Peninsula and considered the influence of pre- and post-fire climate conditions typified through the species' climate niche. To assess forest resilience, we applied the Ecological Dynamic Regime (EDR) framework, a methodological approach to quantify the deviation of disturbed trajectories from their dynamic regimes using three indices: amplitude, recovery and net change. Then, we evaluated how fire characteristics (severity), site attributes (exposure, rockiness) and deviations in the distance to the niche core and edge of the burned populations (centrality–marginality gradient) modulate their resilience to fire.
3. Over 50% of the burned plots exhibited large net change from their dynamic regimes in the midterm, denoting poor resilience regardless of the species' regenerative strategy, and transitioned to shrublands or a different forest type after the fire.
4. Recovery and net change exhibited differences between the two studied species: forests dominated by *P. halepensis* were overall more resilient to fire across the study range, especially in moist sites, while burned *P. nigra* forests showed poor recovery and large net changes after fire. For both species, forest location within the climatic niche before and after fire significantly explained post-fire resilience.
5. In general, forests near their climatic niche core showed higher resilience compared with those close to the dry edge of the niche.

6. *Synthesis*. Our study reveals that post-fire forest resilience depends not only on fire severity and fire characteristics but also on the climatic niche position of the forests. As climate warms and the frequency and intensity of fires increase, forest species will be pushed towards the dry edge of their climatic niches, likely increasing their vulnerability.

KEYWORDS
ecological dynamic regimes, ecological succession, fire, Iberian Peninsula, *Pinus halepensis*, *Pinus nigra*, resilience

1 | INTRODUCTION

Fires are major natural disturbances that promote and accelerate the renewal and change of plant community structure and composition, influence carbon and nutrient cycles, favour some elements of biodiversity and play a crucial role in selecting adaptive traits (Bond & Keeley, 2005; He et al., 2019; McLauchlan et al., 2020; Pausas & Keeley, 2019). The evolutionary coexistence with fires has led plant species in fire-prone ecosystems (e.g. Mediterranean-type regions) to develop adaptations to resist or regenerate after fires (Keeley & Pausas, 2022; Naveh, 1975), through germination (seeder species) or regrowth from surviving tissues (resprouter species). However, fires can also have detrimental effects on fire-adapted ecosystems when their frequency, intensity and extent exceed the adaptive and recovery capacity of the affected ecosystems (Kelly et al., 2020; Nolan et al., 2021; Pausas et al., 2008).

There is growing evidence that climate change is altering fire regimes (Grau-Andrés et al., 2024; Parks & Abatzoglou, 2020; Turco et al., 2018), challenging the post-fire resilience of forests (Coop et al., 2020; Le Breton et al., 2022), understood as the ability to recover their pre-disturbance structure and composition (Holling, 1973). The pre-fire ecosystem state and the characteristics of the fire largely influence post-fire resilience by determining biotic legacies (e.g. seeds or bud banks) and the severity of the disturbance (Johnstone et al., 2016). Resilience also depend on the climatic conditions following the fire and the climate requirements of the affected species (Blanco-Rodríguez et al., 2023; Davis et al., 2019; Karavani et al., 2018). Yet, there are still uncertainties on how pre- and post-fire climate conditions modulate the post-fire resilience across species biogeographical ranges considering a dynamic ecosystem perspective (Seidl et al., 2016). This is a pressing issue in the context of changing climates (Pachauri et al., 2015), which may constrain recovery processes through direct climatic influences on ecosystem dynamics and by increasing climate–disturbance interactions (e.g. fire and drought; Batllori et al., 2019; Turner & Seidl, 2023; Moss et al., 2024).

The species climatic niche offers a powerful conceptual framework for assessing the influence of climatic variability on ecosystem dynamics, incorporating the requirements of the species (Lynch et al., 2014; Margalef-Marrase et al., 2020; Perez-Navarro et al., 2021, 2024; Sexton et al., 2009). The climatic niche refers to the climatic environmental space within which a species is found, encompassing the climatic distribution spanning from the distribution limits (niche edge) to the distribution optimum (niche core) of species (Guisan & Thuiller, 2005; Perez-Navarro et al., 2022). This framework has been successfully used to characterize the influence of pre- and post-disturbance climatic conditions on regeneration success after fire (Elvira et al., 2021, 2025), and to assess the influence of the centrality–marginality of the affected populations (i.e. distance to climatic niche core and edge) in response to other abiotic and biotic disturbances (Jaime et al., 2022; Perez-Navarro et al., 2022).

Ecosystems are constantly undergoing natural fluctuations, with non-equilibrium and transient dynamics being of paramount importance in shaping ecosystem characteristics (Abbott et al., 2021). Consequently, incorporating temporal and spatial variation in the ecosystem state is key to assessing disturbance impacts on ecosystem resilience (Hiers et al., 2012). Assessing changes between the pre-disturbance state, the state immediately following the disturbance and the post-disturbance state (Lloret et al., 2011) requires an explicit consideration of ecological dynamism. Defining ecological trajectories in multidimensional spaces offers a suitable framework to analyse ecosystem dynamics accounting for its heterogeneity and variability (Sánchez-Pinillos et al., 2019). The Ecological Dynamic Regime (EDR) framework (Sánchez-Pinillos et al., 2023, 2024) includes a set of analyses and metrics to assess ecological resilience as the deviation of disturbed trajectories from their respective dynamic regimes (Figure 1a). In this framework, an EDR is defined as a set of trajectories in a multidimensional state space following similar dynamic patterns (e.g. temporal changes in species abundances) under certain environmental conditions and in the absence of perturbations. Then, the ecological resilience of disturbed trajectories is assessed through three indices of amplitude, recovery and net change, which quantify the deviation of the disturbed trajectory from a representative trajectory of a reference EDR (Sánchez-Pinillos et al., 2024). In this way, the EDR framework allows assessing resilience accounting for the fluctuations and variability of ecological systems' dynamics.

Here, we assess the post-fire resilience of Mediterranean forests from a climatic niche and EDR perspective, focusing on two widespread Mediterranean pine species with contrasted post-fire recovery strategies: *Pinus halepensis* Mill. (post-fire serotinous

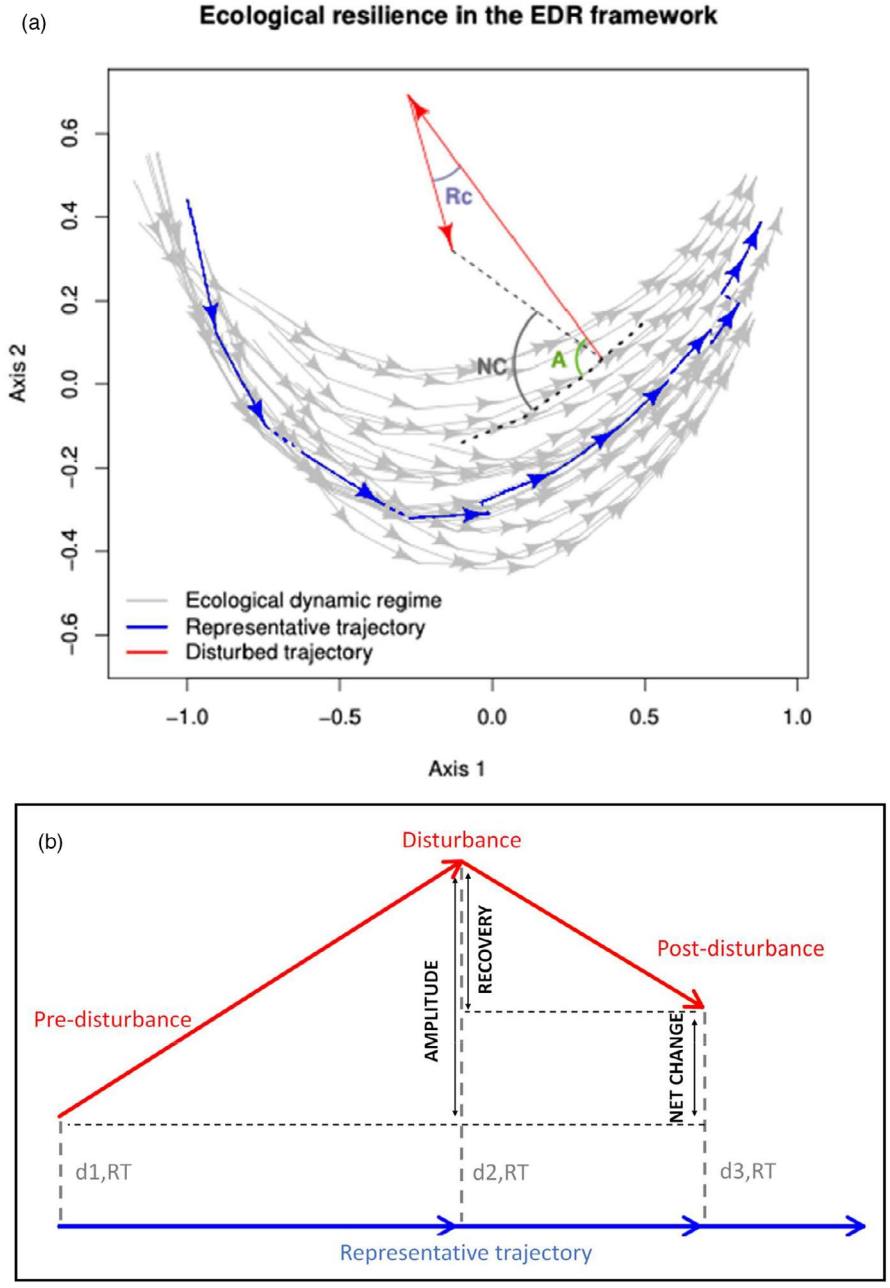

FIGURE 1 (a) In the EDR framework, ecological resilience is evaluated through three indices of amplitude (a), recovery (Rc) and net change (NC), which quantify the deviation (angles) of a disturbed trajectory (red) from an ecological dynamic regime (grey) using a representative trajectory (blue) as the reference. (b) Simplified diagram of the resilience variables calculated from the dissimilarities (*d1,RT*; *d2,RT*; and *d3,RT*) between the states (pre-disturbance, disturbance and post-disturbance) of the disturbed trajectory (red) and the closest states belonging to the representative trajectory (blue).

seeder) and *Pinus nigra* J.F.Arnold (crown fire-sensitive species). We selected two study areas in the Western Mediterranean Basin (Eastern Spain) encompassing a climatic gradient and a broad range of forest structure and composition, and where fire severity and intensity have increased in the last decades (Alvarez et al., 2024; Calheiros et al., 2021). First, we used the community climatic niche approach (Perez-Navarro et al., 2024) to characterize pre- and post-fire climate conditions by determining the position of the burned forests within the climatic niche (distance to the niche core and edge) before and after the fire. Then, we applied the EDR framework (Sánchez-Pinillos et al., 2023, 2024) to quantify the resilience of *P. halepensis* and *P. nigra* burned forests using data from permanent plots of the Spanish National Forest Inventory (SNFI) (Ministerio de Medio Ambiente, 1995, 2007; Ministerio para la Transición Ecológica y el Reto Demográfico, 2024). Finally, we assessed how fire severity and the distance to unburned forests, topographic exposure, soil rockiness, years since fire, and pre- and post-fire climatic conditions influence the resilience of these forests with contrasted recovery strategies. Following the classical niche theory (Hutchinson, 1957; Maguire, 1973) and the 'centrality–marginality hypothesis' (Brown, 1984), we hypothesize that, within the species' climatic niche, pre- and post-fire proximity to the niche edge may hamper forest resilience regardless of species' recovery strategy. Our hypothesis is based on the lower physiological and demographical performance of species close to the climatic distribution limits compared with the distribution optimum (Csergő et al., 2017; Doak & Morris, 2010; Perez-Navarro et al., 2022). This may be particularly relevant in post-fire conditions, because seedlings and saplings are expected to be particularly sensitive to climatic conditions (Grubb, 1977;

Ordoñez-Salanueva et al., 2021; Xu et al., 2022), leading to strong climate–disturbance interactions (e.g. fire and drought) (Batllori et al., 2019; Davis et al., 2019). Additionally, previous studies have shown that post-fire responses can differ across climatic niche space, supporting the application of the niche centrality–marginality framework to fire ecology (Elvira et al., 2021, 2025).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area comprises Mediterranean areas of the Eastern Iberian Peninsula (Figure 2a). Specifically, we have focused on the regions of Catalonia and Murcia, where one pre-fire and two post-fire successive forest inventories (SNFI), resurveyed approximately every 10 years, are available for sites affected by fires between 1991 and 1998 (Figure 2b).

Although geographically close at the regional scale, Catalonia and Murcia have notable differences in their climate and vegetation. Following Rivas-Martínez et al. (2017) the study plots in Murcia are located in the semiarid meso-Mediterranean bioclimate, characterized by an average annual temperature range of 18 to 20°C and low precipitation, typically between 200 and 350 mm per year. In contrast, the plots in Catalonia fall within the dry and sub-humid meso-Mediterranean and the supra-Mediterranean bioclimates. In Catalonia, temperatures vary more widely across the region, with annual averages ranging from 14 to 18°C in the zones with meso-Mediterranean bioclimate, and from 10 to 15°C in the supra-Mediterranean ones. Annual precipitation in Catalonia is also more variable than in Murcia, ranging from 400 to 600 mm in the areas with meso-Mediterranean bioclimate and from 600 to 800 mm in the supra-Mediterranean ones (Rivas-Martínez et al., 2017). The general climatic conditions of the two study regions influence the diversity and structure of the local vegetation, contributing to their distinct ecosystem structure,

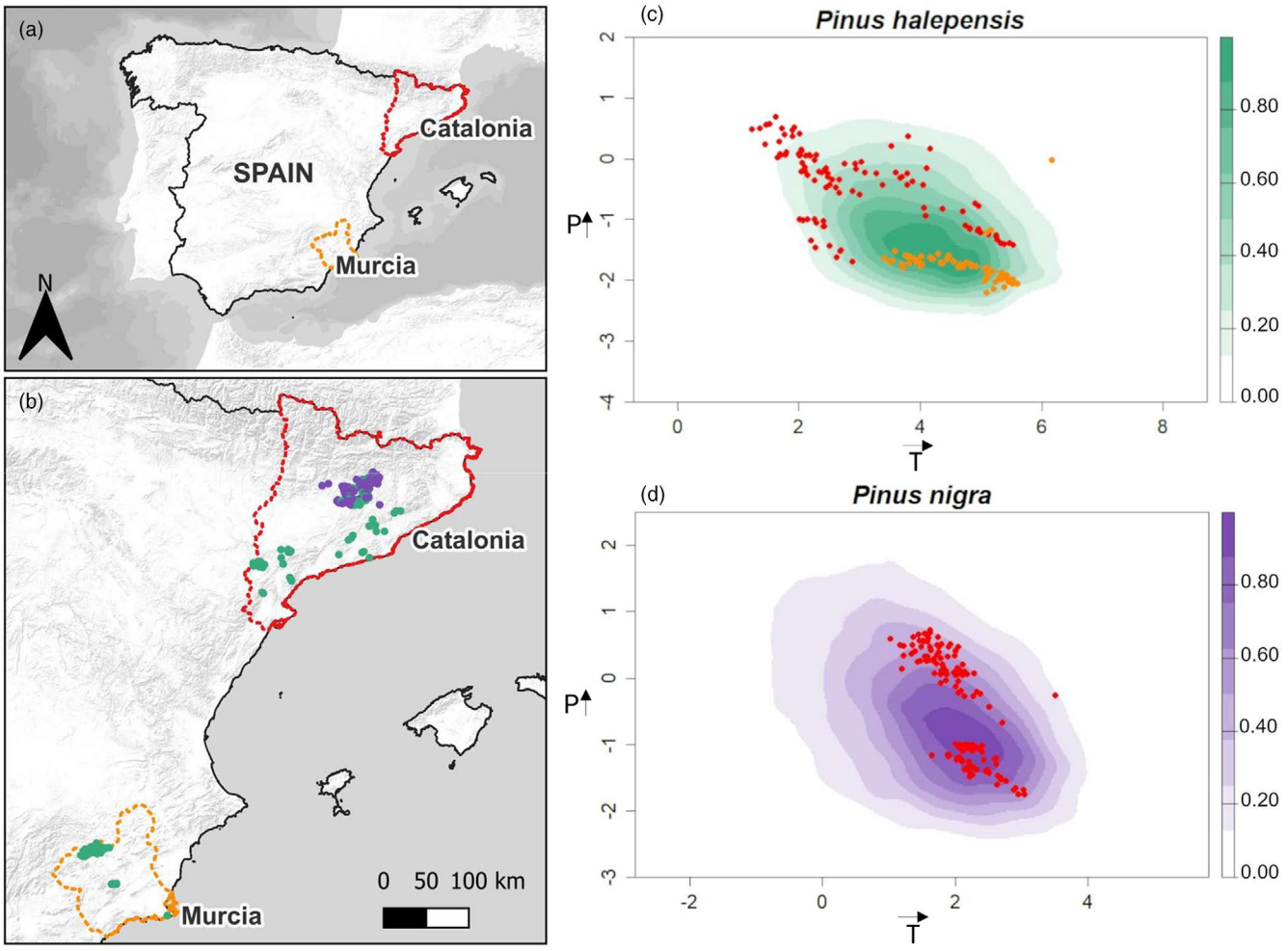

FIGURE 2 (a) Study regions (Catalonia and Murcia) on eastern Spain. (b) Location of burned *Pinus halepensis* (green) and *Pinus nigra* (purple) studied plots in the study region. (c and d) *Pinus halepensis* and *Pinus nigra* climatic niche inferred from their European distribution range (shaded area) and position of the studied plots (points) within the species' climatic niche. Red and orange points correspond to *P. halepensis* plots located in Catalonia and Murcia, respectively. In (c and d), the *X*-axis represents climate variables related to temperature and the *Y*-axis variables related to precipitation; positive values indicate an increase in temperature or precipitation, and negative values indicate a decrease.

composition and ecological dynamics. Murcia has a small forested area (45% of the surface), compared with other regions of the Iberian Peninsula, and low tree diversity (80% surface dominated by *Pinus halepensis*). By contrast, Catalonia is one of the regions of the Iberian Peninsula with the largest forest area (62% of the surface) and greatest tree diversity (including forests dominated by *P. halepensis*, *P. nigra*, *Quercus ilex* L., *Pinus sylvestris* L., *Quercus pubescens* Willd., *Quercus faginea* Lam.; Ministerio para la Transición Ecológica y el Reto Demográfico, 2012, 2017).

2.2 | Study species

We focused on forests dominated by two pine species: *P. halepensis* and *P. nigra*. These pine species cover most of the forest surface affected by fires in the study regions, but exhibit distinct climatic adaptations and occupy different parts of their climatic niches across the study regions. In the case of *P. halepensis*, populations in Catalonia are in the humid part of the species' climatic niche, while in Murcia, they are in the most arid part (Figure 2c; see also 'Climatic niche computation' section below). In the case of *P. nigra* in Catalonia, the species is located in two areas within the niche, roughly corresponding to the zones with meso-Mediterranean and supra-Mediterranean bioclimate (Figure 2d).

Pinus halepensis is a fire-adapted species that usually recovers well after fire, generally contributing to highly flammable vegetation (Fernandes et al., 2008; Ne'eman et al., 2004; Retana et al., 2002). The post-fire recovery capacity of this species largely depends on the abundance of serotinous cones, many of which open with high temperatures, releasing abundant seeds (Espelta et al., 2008) that may profusely germinate after fires. Despite this adaptation, *P. halepensis* shows a great variability in post-fire successful establishment due to, among other factors, water availability for newly established individuals (Pausas et al., 2004), seed predation (Broncano et al., 2008) or competition (De las Heras et al., 2002; Mendez-Cartin et al., 2024).

Pinus nigra is a Mediterranean mountain pine species sensitive to crown fire that does not present adaptations, such as serotiny, to recover after high-severity crown fires (Gil-Tena et al., 2016). However, it has a thick bark that provides effective protection against low-intensity surface fires, allowing adult trees to survive to such events (Espinosa et al., 2020). This species is also vulnerable to drought conditions (Camarero et al., 2013; Gómez-Aparicio et al., 2011), which may further hinder its post-fire regeneration and ultimately reduce its distribution across the Iberian Peninsula (Lloret et al., 2013; Navarro-Cerrillo et al., 2018).

2.3 | Forest inventory and fire data

We used the last three editions of the SNFI dataset in Catalonia and Murcia, consisting of three sequential surveys (SNFI2 1986–1990, SNFI3 1999–2001, SNFI4 2010–2016; Ministerio de Medio Ambiente, 1995, 2007; Ministerio para la Transición Ecológica y el Reto Demográfico, 2024). Surveys were performed using permanent circular plots positioned at the intersections of a $1 \times 1\,km^2$ UTM grid covering all forested areas of the study regions. Each SNFI circular plot encompasses four subplots from 5 to 25 m radius, wherein tree species are inventoried based on their identity and size characteristics. For this study, SNFI data on species identity and diameter at breast height (DBH) were considered for every living tree with a DBH exceeding 7.5 cm within each plot.

Initially, and regardless of the plots' dominant tree species, we selected a total of 266 plots for Catalonia and 77 for Murcia that are comparable across the last three SNFI inventories and where a fire occurred between SNFI2 and SNFI3. The fire georeferenced database (1985–2018) used to select the SNFI plots was obtained from Alvarez et al. (2024). For each plot, we obtained the following states: pre-disturbance (SNFI2), disturbed (SNFI3) and post-disturbance (SNFI4), considering pre-disturbance and post-disturbance periods that ranged between 1 and 9 years (time between the SNFI2 and the fire) and 14 and 25 years (time between the fire and the SNFI4), respectively. To eliminate interferences and when noted in the SNFI database, plots were not considered if they originated from afforestation, if regeneration was not natural after the fires, or when we detected mortalities greater than 20% due to factors other than fire. We also excluded those plots in which more than one fire occurred or other natural or anthropogenic disturbances interfered with the recovery process between SNFI2 and SNFI4.

2.4 | Characterizing forest types

The initially selected SNFI burned plots (266 plots for Catalonia and 77 for Murcia, see Section 2.3) were classified according to their dominant tree species following the procedure described in Sánchez-Pinillos et al. (2021). First, we determined the representative species of burned plots by identifying the dominant and co-dominant tree species on the basis of their relative abundances in the plot, considering the basal area (BA) of adult trees and saplings. The same procedure was applied to all (burned and unburned) SNFI plots in the study regions ($N = 16{,}069$ plots) to assess those plots with a relative abundance >20% for at least one representative tree species, or where the sum of the relative abundances of the plots' representative tree species exceeded 50%. Finally, we employed a cluster analysis based on the dissimilarities in species composition to classify SNFI plots based on the dominance of their representative tree species. To achieve this, we constructed a symmetric squared matrix capturing the percentage difference (i.e. the Bray–Curtis dissimilarity) between all plots and surveys using species BA as the abundance variable. Subsequently, we used the algorithm Partition Around Medoids (PAM) (Kaufman & Rousseeuw, 1990) to classify each SNFI survey. The optimal number of clusters (i.e. forest types) in the range from 2 to 10 was selected using the Silhouette analysis (Kaufman

& Rousseeuw, 1990). We made the process separately for the two study regions. The clustering procedure allowed us to retain burned plots dominated or co-dominated by *P. halepensis* (67 in Murcia and 76 in Catalonia) and *P. nigra* (115 in Catalonia). Those plots encompass a total of 19 different tree species (Appendix S1: Table S1).

2.5 | Climatic niche characterization and position in niche space

To characterize the climatic niche of the 19 tree species present in the burned plots (dominated by *P. halepensis* and *P. nigra*), we used their European geographic distribution and inter-annual climatic variability extracted from their spatial locations. Species occurrence data were collected from EUForest (Mauri et al., 2017) with occurrences ranging from 156 to 75,720 among species, considering a 1 km pixel spatial resolution. Climatic data were obtained from CHELSA (Brun et al., 2022; Karger et al., 2017): bio1 (mean annual air temperature), bio4 (temperature seasonality), bio5 (mean daily maximum air temperature of the warmest month), bio6 (mean daily minimum air temperature of the coldest month), bio10 (mean daily mean air temperatures of the warmest quarter), bio11 (mean daily mean air temperatures of the coldest quarter), bio12 (annual precipitation amount), bio13 (precipitation amount of the wettest month), bio14 (precipitation amount of the driest month), bio15 (precipitation seasonality), bio16 (mean monthly precipitation amount of the wettest quarter), bio17 (mean monthly precipitation amount of the driest quarter), bio18 (mean monthly precipitation amount of the warmest quarter), PET (mean annual potential evapotranspiration) and VPD (mean annual vapour pressure deficit).

For each location of the species occurrence datasets we extracted yearly climate values from 1979 to 2010, rather than using average values for the entire period, to incorporate the inter-annual variability in the environmental conditions experienced by the species (Perez-Navarro et al., 2021). We then employed principal component analysis (PCA) to transform the standardized environmental data encompassing the 15 bioclimatic variables into a two-dimensional climatic space, defined by the first and second principal components. This PCA incorporated climatic data from each year across all occurrence sites for all 19 species. Together, the first and second principal components explained 75.5% of the variability of the original variables, with the first axis (49.4%) mostly representing temperature-related variables and the second axis (26.1%) representing precipitation-related variables (Appendix S1: Figure S1).

To characterize the climatic niche of each tree species included in our analyses, we calculated the density of their occurrences within the PCA climatic space using kernel density functions (Broennimann et al., 2012; R package ks, Chacón & Duong, 2018). Then, we estimated the position of the niche core or optimum, defined as the centre of gravity of the species niche (assuming that it is the point with the highest density of occurrences), and of the climatic niche edge or limit, set at the 0.05 lowest percentile of occurrences density (Perez-Navarro et al., 2022).

The inter-annual climatic variability of each SNFI plot reflecting climatic conditions before and after the fire event was also translated into the species climatic niche space. Specifically, we considered two time periods: midterm (10 years window) before the fire, and immediate (3 years window) before and after the fire. Subsequently, for each species in each plot and for all years within the pre- and post-fire periods considered, we computed the Euclidean distance to: (1) the climatic niche core and (2) the closest point of the niche edge of the respective species. We classified species' occurrences based on their placement 'inside' or 'outside' of the species climatic niche, with negative distance being assigned to 'outside' occurrences.

To derive climatic niche indices (distance to niche core and edge) at the plot level, we calculated the tree community weighted distance to the climatic core (DCC) and edge (DCE), weighting the niche distances according to the relative abundance of the species in each plot. We calculated the DCC and DCE immediate pre-fire by averaging the distances of the 3 years before the fire (DC3_pre: immediate pre-fire distance to core; DE3_pre: immediate pre-fire distance to the edge), the DCC and DCE immediate post-fire by averaging the distances of the 3 years after the fire (DC3_post: immediate post-fire distance to core; DE3_post: immediate post-fire distance to the edge), and the DCC and DCE midterm pre-fire by averaging the distances of the 10 years before the fire (DC10_pre: midterm pre-fire distance to core; DE10_pre: midterm pre-fire distance to edge).

To evaluate the influence of the specific climatic niche edges, we calculated the distance from each plot to the dry and moist edges of the climatic niche of their dominant species (*P. halepensis* or *P. nigra*). We first divided the two-dimensional PCA-derived climatic space into four quadrants based on the climatic niche centroid. Considering the distribution of temperature and precipitation variables in each PCA axis, we identified the quadrants representing dry, moist and intermediate climatic conditions. The dry and moist niche limits were defined as the species' niche limit sections comprised in the dry and moist quadrants, respectively (Appendix S1: Figures S2 and S3). These edge definitions allowed us to compute, for each studied plot and time period (10 years before fire, 3 years before fire and 3 years after fire), the Euclidean distance to the nearest dry and moist edge of the dominant species niche. Finally, we grouped plots into two categories (dry and moist) according to which niche edge they were closest.

2.6 | Assessing resilience based on ecological dynamic regimes

To evaluate the resilience to fire of the forest types assessed here, we applied the methodological framework developed by Sánchez-Pinillos et al. (Sánchez-Pinillos et al., 2023, 2024), which is based on EDRs. Overall, the assessment of resilience following the EDR framework comprises three steps: (1) definition of the EDRs of the systems of interest; (2) computation of a representative trajectory

passing by the densest regions of each EDR; and (3) calculation of the indices of amplitude, recovery and net change that permit comparing the disturbed trajectories with the representative trajectory of the corresponding EDR (Sánchez-Pinillos et al., 2024).

2.6.1 | Definition of ecological dynamic regimes

We defined a distinct EDR for *P. halepensis* and *P. nigra* dominated forests using all the SFNI plots within each region of the study area that were classified as one of these two forest types (see Section 2.4, Table S1) and in which there was no evidence of disturbances, including fires and silvicultural practices. The EDRs of each forest type were defined as a set of undisturbed trajectories classified as *P. halepensis* or *P. nigra* forests in at least one out of the three trajectory states (i.e. SFNI surveys). Each EDR was composed of 1321 (*P. halepensis* in Murcia), 2048 (*P. halepensis* in Catalonia) and 1446 trajectories (*P. nigra* in Catalonia), each with two or three states depending on the data availability. In the EDR we considered species other than *P. nigra* and *P. halepensis* (Appendix S1: Table S1) and states with other forest types (forests dominated by *Q. faginea*, *Q. ilex*, *Q. suber*, *P. pinea* or *P. sylvestris*) (Appendix S1: Figure S4).

2.6.2 | Computation of representative trajectories

To generate the representative trajectories of each EDR (Figure 1a), we first required a dissimilarity matrix of the different plots and surveys. Employing DBH as a structural variable and BA as a measure of abundance, we reshaped forest plot data from individual trees into a stratified form to calculate cumulative abundance profiles (De Cáceres, 2012) and to build a new matrix for each plot survey. These matrices were used to calculate the dissimilarity matrices using an adapted version of the Bray–Curtis metric (De Cáceres et al., 2013), thus obtaining the state dissimilarity matrix.

Then, we calculated a set of representative trajectories by applying the RETRA-EDR (Representative Trajectories in Ecological Dynamic Regimes) algorithm Sánchez-Pinillos et al. (2023) on the resulting dissimilarity matrix. For that, we used the R package 'ecoregime' (Sánchez-Pinillos et al., 2023, 2024) using 5% of the number of states in each EDR to define the minimum number of trajectory segments to be represented by each segment of the resulting representative trajectories.

In some cases, we identified more than one representative trajectory per EDR. In these cases, we evaluated each trajectory and selected the most suitable one based on the statistics returned by RETRA-EDR, such as the size of each representative trajectory, the number of partitions associated with each representative segment (i.e. *kdTree depth*), and the length of artificial links (see Sánchez-Pinillos et al., 2023 for details).

2.6.3 | Amplitude, recovery and net change

Finally, we evaluated forest resilience by analysing their dynamic responses to fire by calculating three complementary indices: amplitude, recovery and net change (Figure 1b), which quantitatively assess the dissimilarities of the different states of the disturbed plots to the representative trajectory (Sánchez-Pinillos et al., 2024). Within the EDR framework, these indices allow capturing the natural fluctuations of the system and, therefore, better characterize the ecological resilience.

Amplitude represents how much the disturbance moves the affected plots away from (or towards) the representative trajectory, relative to the position of the pre-disturbance state (i.e. SNFI 2) (Sánchez-Pinillos et al., 2024). So,

$$\text{Amplitude} = d_{2,\text{RT}} - d_{1,\text{RT}}$$

where $d_{1,\text{RT}}$ is the dissimilarity between the pre-disturbed state (i.e. SNFI 2) and the representative trajectory, $d_{2,\text{RT}}$ is the dissimilarity between the disturbed state (i.e. SNFI 3) and the representative trajectory (Figure 1b). In our study, $d_{1,\text{RT}}$ and $d_{2,\text{RT}}$ were calculated as the dissimilarity of the pre-disturbed and disturbed state to their nearest state in the representative trajectory. Therefore, based on the dissimilarity metric that we used, amplitude ranges between −1 and 1, indicating that the system goes further (positive values) or closer (negative values) to one of the states in the representative trajectory. Negative amplitude values indicating that the disturbance moves the system closer to the representative trajectory may occur in forests affected by selective disturbances impacting specific components of the system (e.g. pests, pathogens or thinning); however, we do not expect to observe negative amplitude values in forests affected by severe fires. Positive and high values of amplitude (close to 1) could be understood as a lack of resistance of the system to remain within the dynamic regime during the disturbance. Importantly, this index refers to the deviation of the system (positive or negative) with respect to a representative trajectory and must not be confused with the resistance index proposed in the EDR framework to quantify the direct effects of the disturbance on the state variables (Sánchez-Pinillos et al., 2024).

Recovery indicates how the last assessed post-disturbance state (SNFI 4) has changed relative to the position of the disturbed state (SNFI 3) in relation to the representative trajectory. Therefore, it measures the ability of the disturbed plots to become closer to the representative trajectory (Sánchez-Pinillos et al., 2024). So,

$$\text{Recovery} = d_{2,\text{RT}} - d_{3,\text{RT}}$$

where $d_{3,\text{RT}}$ in our study was calculated as the dissimilarity between the post-disturbance state (i.e. SNFI 4) and the nearest state of the representative trajectory (Figure 1b). Recovery ranges from −1 (the trajectory is becoming farther from the nearest state of the representative trajectory after the disturbance) to 1 (the trajectory is becoming closer to one of the states of the representative trajectory), with 0 indicating no recovery after the disturbance.

Net Change indicates how the last assessed post-disturbance state (SNFI 4) has changed relative to the position of the pre-disturbance state (SNFI 2) in relation to the representative trajectory (Figure 1b; Sánchez-Pinillos et al., 2024). So,

$$\text{Net Change} = d_{3,RT} - d_{1,RT}$$

Net change ranges from −1 (the trajectory is becoming closer to one of the states of the representative trajectory) to 1 (the trajectory is becoming farther to the states of the representative trajectory), with 0 indicating that the post-disturbance state remains at the same distance to a state of the representative trajectory than it was before being disturbed, regardless of the identity of the nearest states of the pre-disturbance and post-disturbance states.

Although amplitude, recovery and net change can appear related to other indices previously defined to assess engineering resilience based on a pre-disturbance state (e.g. resistance, recovery and resilience, respectively, in Lloret et al., 2011), they cannot be confused since they refer to a dynamic regime in which a representative trajectory is recognized.

2.6.4 | Definition of resilience failure

In this study, we considered a potential failure in forest resilience when net change values were greater than 0.25. Then, we determined the pattern behind resilience failure in each case: (i) low recovery of the tree community, when recovery was observed (i.e. recovery >0) but the rate was so low that the net change was high (>0.25); (ii) forest shift, when the initial forest state (SNFI2) changed to a different forest category based on tree species dominance in the post-disturbance state (SNFI4); or (iii) change to shrubland, when tree species did not recover and there was only the presence of shrub coverage in the post-disturbance state (according to the values obtained from SNFI 4). The net change value of 0.25 was arbitrarily chosen to establish a threshold to study potential causes of resilience failure; it is important, however, to note that our dataset did not allow us to discard the recovery of the system on longer temporal scales than considered here.

2.7 | Fire severity and environmental variables

Fire severity was calculated from Landsat-based fire severity maps using the Google Earth Engine (GEE) platform following Parks et al. (2018). As described in Alvarez et al. (2024), we applied the relativized delta normalized burn ratio (RdNBR) (Miller & Thode, 2007), that analyses the vegetation state before and after fire with satellite images, using the mean compositing approach, where all cloud-free pixels from September to October for the year previous to the fire and the year of the fire are stacked and the mean value for each pixel over the stack is used to compute fire severity. When September–October images were not available, we expanded the period to November. For each burned plot, we calculated the closest geographical distance to unburned forests of the same forest type using their distribution areas as defined in the Forest Map of Spain (MFE50) (1997–2006) and also considering unburned forest areas within fire polygons. We used RdNBR because it incorporates pre-fire vegetation characteristics through the use of pre-fire NBR values, and is not too sensitive to spatial variation in vegetation type, structure and canopy cover, an essential property for heterogeneous Mediterranean landscapes (Botella-Martínez & Fernández-Manso, 2017; Miller & Thode, 2007; Parks et al., 2014).

The rest of explanatory variables considered in our analysis included the following: fire ID and years since fire, calculated from the fire year and the SNFI3 and SNFI4 sampling year; plot exposure measured as solar radiation, as obtained from CHELSA (Karger et al., 2017); and plot rockiness, as provided by the SNFI database (Ministerio para la Transición Ecológica y el Reto Demográfico, 2024).

2.8 | Statistical analysis

We performed linear mixed models (LMM) to assess the relationships between the resilience indices of amplitude, recovery and net change (dependent variables), and the weighted distances in climatic niche space (DCC and DCE), fire severity (RdNBR), years since fire, distance to unburned forest, rockiness and exposure (srad) as explanatory variables. Fire ID was included as a random effect within the models.

Models were performed, both with and without interactions, separately by each forest type. The final model for each resilience index and forest type was selected based on the ecological significance of the variables refined through stepwise selection method, using the Akaike information criterion (AIC) and their R^2 (marginal and conditional) values (Appendix S1: Tables S2–S4). In addition, we tested the residuals to analyse the quality of the models using the DHARMa package (Hartig & Hartig, 2022), which performs different analyses such as the Kolmogorov–Smirnov uniformity test, dispersion test, outlier test and graphical analyses like Q-Q plot residuals and nonparametric dispersion tests via the standard deviation of residuals fitted vs. simulated, to assess whether the residuals of the model follow a normal distribution.

In addition, we performed the Wilcoxon rank-sum test to explore the relationships between the resilience indices (amplitude, recovery and net change) and the plots' distances to the dry and moist climatic niche edges for both *P. halepensis* and *P. nigra*, considering the three pre- and post-fire periods (10 years before and 3 years before and after fire). This allowed us to assess whether resilience to fire (amplitude, recovery and net change) varies between the dry and moist portions of the climatic niche.

All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022).

3 | RESULTS

Fires, as expected, pushed most of the affected forests away from their representative successional trajectory (Figures 2a and 3, Appendix S1: Figures S5–S7), as indicated by the mostly

positive amplitude values. No significant differences in amplitude were observed between forest types (*P. halepensis* and *P. nigra*) or between regions for a given forest type (*P. halepensis* forests in Murcia and Catalonia). Amplitude values ranged between 0.758 ± 0.305 (mean ± standard deviation) for *P. halepensis* in Murcia, 0.721 ± 0.295 for *P. halepensis* in Catalonia and 0.761 ± 0.269 for P. nigra in Catalonia. By contrast, significant differences appeared in the recovery ability of the burned forests, contingent on species and study region (Figure 3). In Murcia, the most arid region, *P. halepensis* plots exhibited low, but positive, recovery after fire (mean value = 0.248 ± 0.15 SD), with only 37.3% of them moving back towards the representative trajectory after being disturbed (recovery >0). In Catalonia, *P. halepensis* forests showed significantly higher values of recovery (mean value = 0.371 ± 0.366 SD) and, despite the high variability, 80.3% of plots moved back towards the representative trajectory after fire. Recovery in *P. nigra* forests in Catalonia was also positive but low (mean value = 0.125 ± 0.287 SD), with 57.4% of the plots approaching the representative trajectory after the fire. Finally, the net ecosystem change induced by fire was significantly different between forest types and regions (Figure 3). The *P. halepensis* forests in Catalonia exhibited significantly lower, yet positive, values of net change (mean value = 0.35 ± 0.339 SD) compared with *P. halepensis* in Murcia (mean value = 0.633 ± 0.369 SD) and *P. nigra* in Catalonia (mean value = 0.61 ± 0.342 SD). Therefore, despite forest types in the study regions exhibiting similar deviations from the representative trajectory due to fire (i.e. no significant differences in amplitude), *P. halepensis* forests in Catalonia showed the smallest deviations from the representative trajectory at the post-disturbance state (SFNI4) in relation to the pre-disturbance state (SFNI2) (Figure 3).

We found a potential failure of resilience (net change values >0.25) in a high number of plots (48.7% of *P. halepensis* in Catalonia, 77.6% of *P. halepensis* in Murcia and 80% of *P. nigra* in Catalonia), the change from forest to shrubland being the main cause of resilience failure (Figure 3; Table 1). Additionally, 31.3% of the *P. nigra* burned forests did not return to the representative trajectory but transitioned to forests dominated by oaks (*Q. ilex* and *Q. faginea*; Table 1; Appendix S1: Figure S7). In Catalonia, post-fire shifts of burned *P. halepensis* forests to other forest types were also observed, representing 15.8% of the burned plots, largely due to oak's increase (Table 1; Appendix S1: Figure S6).

Explanatory models indicated that pre- and post-fire climate conditions typified through the climatic niche, together with fire severity, were significantly related to forest resilience to fire (Figure 4). The midterm distance to the niche edge describing pre-fire climatic conditions (mean of 10 years window) appeared significant in most of the models, regardless of forest type. Other explanatory variables

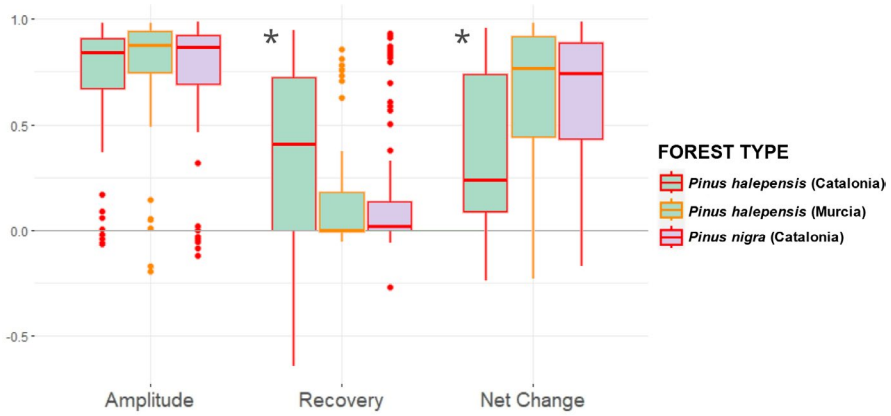

FIGURE 3 Comparison of the values of resilience indices (amplitude, recovery and net change) between forests dominated by *Pinus halepensis* in Catalonia, *P. halepensis* in Murcia, and *P. nigra* in Catalonia. Boxes' lower and upper hinges show the 25%–75% percentile range, and boxes' horizontal lines correspond to the median value for each resilience metric. Asterisk indicates significant differences ($p < 0.001$) between *P. halepensis* forests in Catalonia and the other forest types (Tukey's test).

TABLE 1 Comparison of the responses of the burned plots of *Pinus halepensis* and *P. nigra* in Catalonia and Murcia.

						Causes of potential resilience failure (Net change >0.25)		
Dominant species	Region	No. of SNFI plots	Burned SNFI plots	Recovery >0	Net change >0.25	Low recovery	Forest shift	To shrub
Pinus nigra	Catalonia	2654	115	66 (57.4%)	92 (80%)	7 (6.1%)	36 (31.3%)	49 (42.6%)
Pinus halepensis	Catalonia	4859	76	61 (80.3%)	37 (48.7%)	10 (13.2%)	12 (15.8%)	15 (19.7%)
Pinus halepensis	Murcia	948	67	25 (37.3%)	52 (77.6%)	10 (14.9%)	0 (0%)	42 (62.7%)

Note: The total number of Spanish National Forest Inventory plots (SNFI) and the number of burned plots per species and region is shown. We consider that plots return to the representative trajectory when their recovery shows positive values (Figure 3). We consider that values higher than 25% of net change (>0.25) indicate potential resilience failure associated with low recovery rates of the tree community, forest shifts or changes to shrubland. Proportions in parenthesis refer to the number of burned plots per species and region.

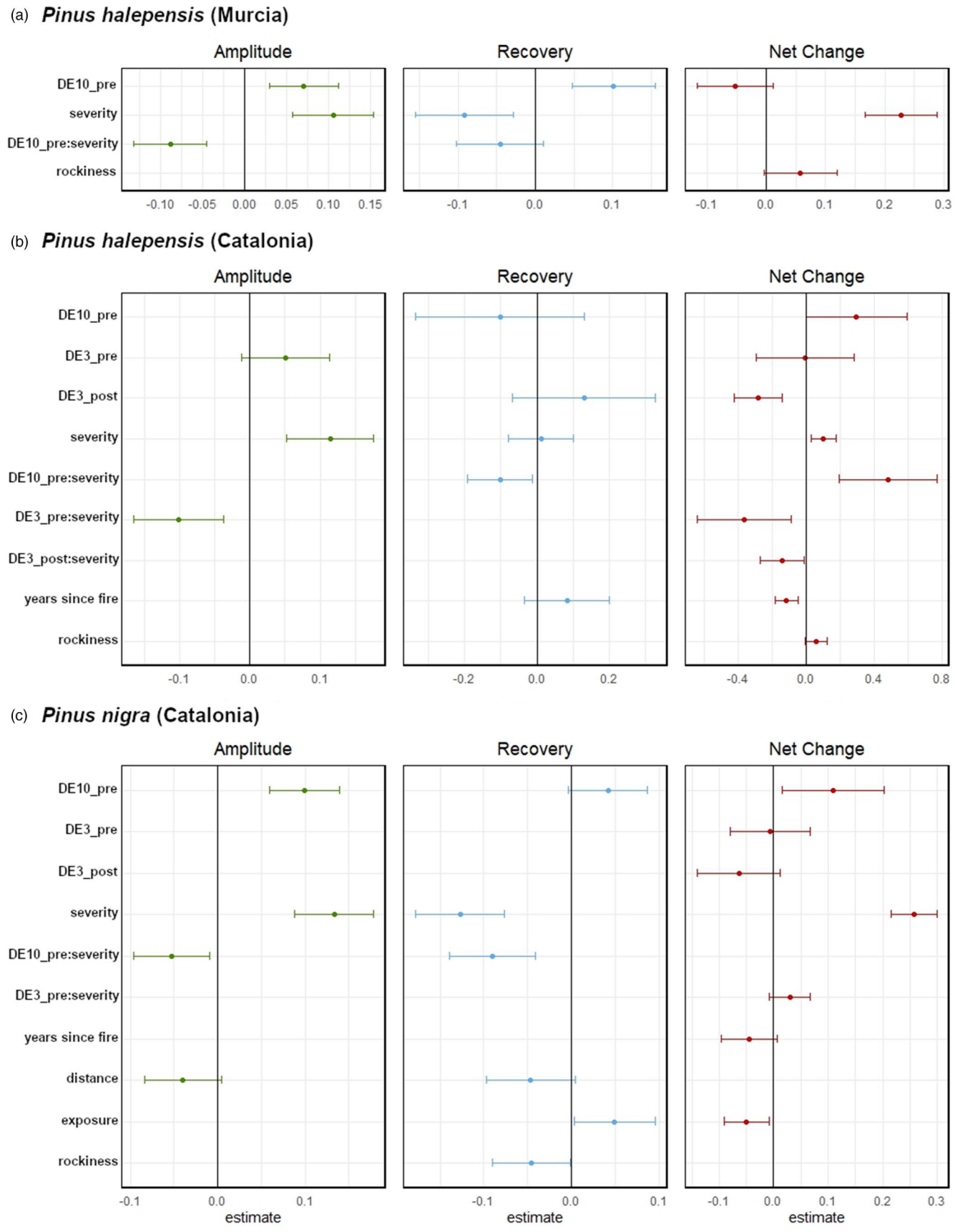

FIGURE 4 Estimated linear mixed model coefficients (95% confidence intervals) for the resilience metrics amplitude, recovery and net change, as a function of climatic, fire and environmental variables and the interactions between them (DE3_pre: immediate pre-fire distance to the climatic niche edge; DE3_post: immediate post-fire distance to the climatic niche edge; DE10_pre: midterm pre-fire distance to climatic niche edge) for: (a) *Pinus halepensis* in Murcia, (b) *Pinus halepensis* in Catalonia and (c) *Pinus nigra* in Catalonia.

had a significant effect on forest resilience metrics in univariate models (Appendix S1: Tables S12, S13 and S16), including terrain exposure (p-value <0.02) and distance to unburned forests (p-value <0.01), although they were not significant in the final models (Figure 4).

Fire severity had a significant and positive relationship with amplitude in all forest types (Figure 4). Its interaction with midterm or immediate distance to the niche edge before the fire (DE10_pre and DE3_pre, respectively) also showed a significant effect on amplitude: *P. halepensis* in Murcia (DE10_pre:severity, p-value <0.001), *P. halepensis* in Catalonia (DE3_pre:severity, p-value <0.01) and *P. nigra* in Catalonia (DE10_pre:severity, p-value <0.02). At low fire severities, the plots closer to the climatic niche edge showed less amplitude than the plots closer to the niche core, while at high fire severities the amplitude is high regardless of the distance to niche edge (Figure 5, Appendix S1: Figure S8).

For recovery, we found a significant interaction of fire severity with DE10_pre for *P. halepensis* (p-value <0.03) and *P. nigra* (p-value <0.001) in Catalonia. At low fire severities, the recovery is higher near the niche core than the niche edge in the *P. nigra* forest types (Figures S9), but *P. halepensis* recovery remains constant at low levels (Figure 5). At high fire severities, *P. halepensis* forests showed lower recovery close to the niche core than to the niche edge, whereas *P. nigra* recovery remains constant at low levels regardless of the distance to the niche edge (Appendix S1: Figure S9).

Fire severity had a significant and positive relationship with net change in all forest types (Figure 4). We only found a significant influence of the interaction between fire severity and pre- and post-fire conditions for the net change of *P. halepensis* forests in Catalonia. At low fire severities and considering midterm pre-fire conditions (DE10_pre), net change was higher close to the niche edge than to the niche core, whereas at high fire severities net change was lower close to the niche edge than to the niche core (Figure 5). When considering immediate pre- and post-fire conditions (DE3_pre and DE3_post, respectively), we observed reversed effects of severity on net change (Figure S10); net change was lower close to the niche edge than the niche core at low severities and it was higher close to the niche core than to the niche edge at high fire severities. Finally, the net change of *P. nigra* and *P. halepensis* in Catalonia was negatively related to the length of the recovery period (i.e. the years since fire), although this relationship was only significant for *P. halepensis* forests.

We observed consistent differences between moist and dry climatic niche edges across resilience indices, especially for *P. halepensis* (Table 2). For *P. halepensis*, amplitude was significantly higher closer to the dry edge of the climatic niche compared with the moist edge, when considering the conditions both before and after fire (Table 2, Figure S11). Recovery was significantly higher closer to the moist edge in *P. halepensis*, considering the conditions before and after fire (Table 2, Figure S11). In contrast, net change showed the opposite pattern to recovery, with higher values closer to the dry edge of the niche (Table 2, Figure S11). For *P. nigra*, the relationships were weaker and only associated with recovery and net change, and suggested differential effects of pre- and post-fire climate conditions (Table 2, Figure S12). Recovery was slightly higher closer to the dry edge, when considering only the climatic conditions after fire. Conversely, net change was higher closer to the moist edge when considering the climatic conditions before fire, while the opposite relationship was observed when considering the post-fire period (Table 2, Figure S12).

4 | DISCUSSION

Over 50% of the burned forests showed low post-fire resilience in terms of a high degree of net ecosystem change within the study period, regardless of species recovery strategy and study region (Table 1). The main cause of potential resilience failure was a shift from forest to shrubland, dominated mainly by *Salvia rosmarinus* (L.) Schleid. and *Quercus coccifera* L. (by *Cistus clusii* Dunal also in Murcia) (according to SNFI4 data, Ministerio para la Transición Ecológica y el Reto Demográfico, 2024), especially for forest located close to the dry edge of the species' climatic niche. Shifts to other forest types, mostly with abundance of *Quercus* sp. pl., were also important in burned *P. nigra* forests. However, the observed resilience failure may not necessarily imply permanent state changes, as they may encompass slow tree recovery rates relative to the surveyed period, or transitional turnover in tree species composition. Additionally, we found significant differences in the factors related to the amplitude, recovery capacity and net change in response to fire severity, contingent on species climatic requirements and study region. Overall, our study shows that the integration of climatic niche characterization with the EDR framework provides valuable information for assessing and quantifying the post-fire resilience of forest ecosystems in relation to climatic variability.

The EDR framework (Sánchez-Pinillos et al., 2023, 2024) allowed us to assess the post-fire resilience of different forest types fires considering their dynamics. Using representative trajectories instead of particular pre-disturbance states as reference allowed us to account for the successional changes of the system, and to determine whether burned forests remained relatively close to the reference trajectory of its dynamic regime (indicating resilience; 29.8% of the plots with net change <0.25) or failed to return to it (indicating lack of resilience; 70.2% of the plots with net change >0.25). It is important to note, however, that our analyses were limited by the availability of long-term data. The SNFI inventories covered up to 25 years after fire (mean value = 17.23 ± 2.42 SD), and such a relatively short time span very likely contributed to the observed resilience failure (high net change values). Besides, we defined forest dynamic regimes from the dominance of tree species instead of considering similarities also including shrub species. As such, the post-disturbance plots dominated by shrublands could actually belong to the forest dynamic regimes. Thus, despite the observed changes in species composition after fire, additional assessments are needed to confirm whether those correspond to low resilience rates (based on amplitude, recovery and net change) or to shifts into alternative dynamic regimes.

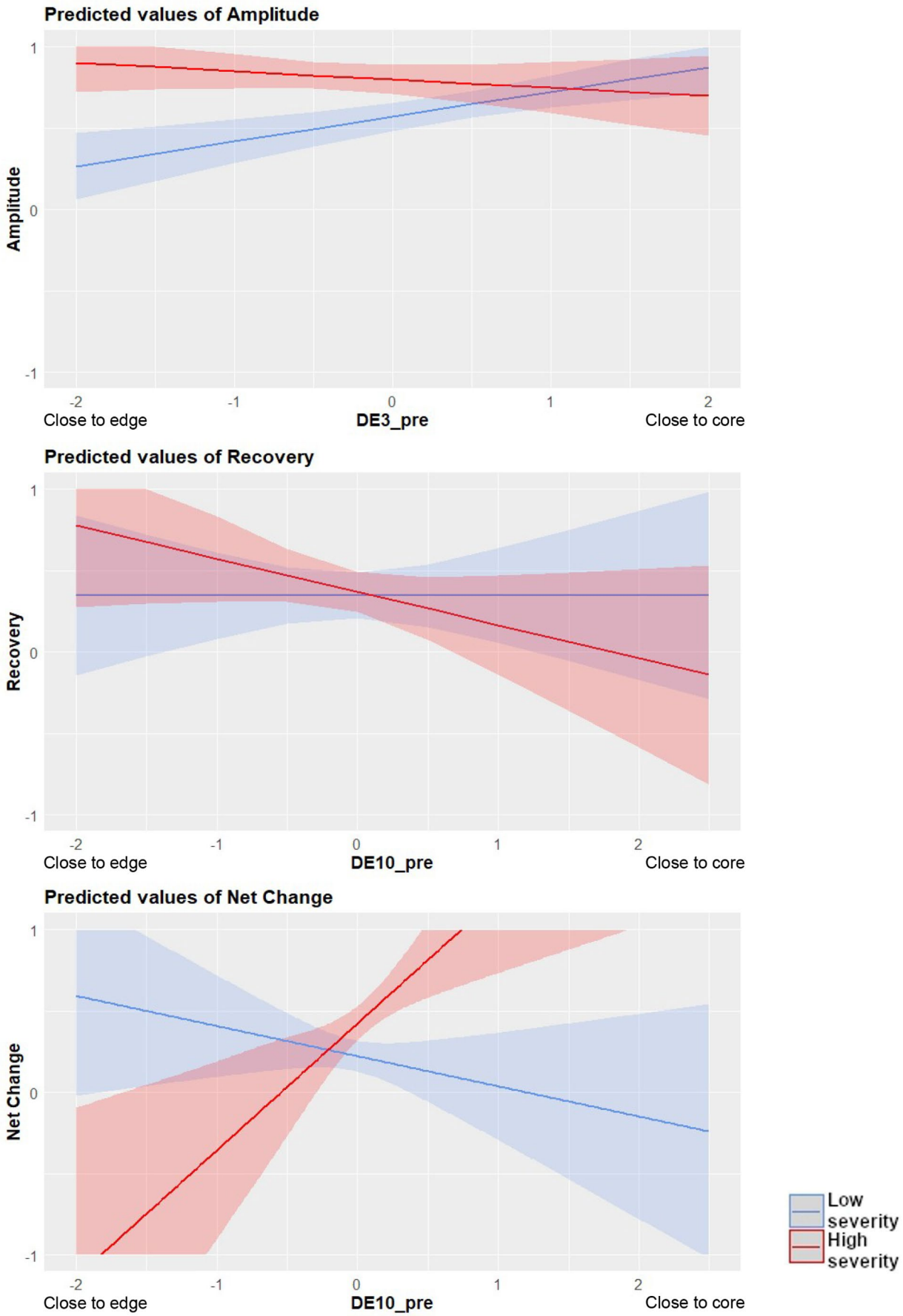

FIGURE 5 Effect of the interaction between fire severity (RdNBR) and distance to the climatic niche edge immediate pre-fire (DE3_pre) and midterm pre-fire (DE10_pre) in relation to amplitude, recovery and net change values in forests dominated by *Pinus halepensis* in Catalonia. (DE3_pre: immediate pre-fire distance to the edge; DE10_pre: midterm pre-fire distance to edge).

TABLE 2 Mean ± standard deviation of resilience metrics (amplitude, recovery and net change) in relation to the distance to moist and dry climatic niche edges for *Pinus halepensis* and *Pinus nigra*, across three periods relative to fire (10 years before, 3 years before, and 3 years after fire).

		Pinus halepensis			*Pinus nigra*		
		Moist	Dry	*p*-value	Moist	Dry	*p*-value
10 yr_pre	Amplitude	0.69 ± 0,32	0.76 ± 0.29	0.043*	–	–	–
	Recovery	0.39 ± 0.34	0.18 ± 0.31	0.002**	–	–	–
	Net change	0.3 ± 0.3	0.58 ± 0.38	<0.0001***	–	–	–
3 yr_pre	Amplitude	0.69 ± 0.31	0.77 ± 0.29	0.03*	0.84 ± 0.12	0.72 ± 0.31	0.08
	Recovery	0.38 ± 0.34	0.18 ± 0.32	0.003**	0.11 ± 0.25	0.17 ± 0.3	0.103
	Net change	0.31 ± 0.32	0.58 ± 0.38	<0.0001***	0.73 ± 0.26	0.55 ± 0.37	0.009**
3 yr_post	Amplitude	0.7 ± 0.31	0.76 ± 0.29	0.033*	0.73 ± 0.3	0.8 ± 0.23	0.368
	Recovery	0.39 ± 0.34	0.17 ± 0.31	0.0006***	0.18 ± 0.3	0.12 ± 0.28	0.023*
	Net change	0.31 ± 0.31	0.6 ± 0.38	<0.0001***	0.55 ± 0.35	0.68 ± 0.33	0.022*

Note: Differences between moist and dry niche positions were assessed using Wilcoxon rank-sum tests, and associated *p*-values are reported. Significance levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. In the case of *P. nigra* during the 10 yr_pre period, all plots were closest to the dry niche edge; therefore, differences between moist and dry regions could not be assessed.

Populations' climatic marginality in niche space before and after the fire, and its interaction with fire severity, strongly modulated post-fire resilience patterns. This reinforces the idea that the climatic niche framework in conjunction with disturbance attributes can improve our understanding of ecosystem resilience (Elvira et al., 2021, 2025). Importantly, the specific influence of pre- and post-fire climatic marginality on forest resilience is related to the ecological and biological characteristics of the involved species. Still, the midterm pre-fire climate (10 years window before fire) exerted, overall, the strongest influence on the resilience capacity of the species under study. This is consistent with the fact that post-fire recruitment of seeder species, which depends on seed availability, highly depends on pre-fire weather conditions suitable for reproductive success (Nolan et al., 2021; Ooi et al., 2014). Additionally, while it is evident from previous studies that post-fire resilience is influenced by climatic conditions (e.g. Besnard et al., 2019; Hao et al., 2022), our assessment highlights that, for a given forest type, specific responses to fires also depend on species composition and the position of burned populations within the tree community-level climatic niche (Figure 4).

Despite the supposed inherent resilience of many Mediterranean forests, our study demonstrated that fires often hinder or prevent their midterm recovery. Our assessment shows that fire severity is significantly related to lower values of recovery and higher values of ecosystem amplitude and net change, and therefore, it determines low resilience overall (Figure 4). This is in line with previous studies indicating the importance of fire severity in constraining post-fire recovery of Mediterranean forests (Fernández-García et al., 2019; González-De Vega et al., 2018; Pausas et al., 2002; Viana-Soto et al., 2017) due to its effects on biological remnants (i.e. seed and bud banks) or in soil properties determining water and nutrient uptake (Fernández-García et al., 2020). The negative influence of fire severity on forest resilience together with the reported trends of increased fire intensity and severity in the study area (Alvarez et al., 2024), raises concerns about the resilience capacity of Mediterranean pinewoods under climate change. In addition to severity, the relationship between other fire regime components such as fire frequency and position in climatic niche space merits further consideration in future assessments. The interactions between pre- and post-disturbance climate and fire severity (Figure 4) observed for most resilience metrics further highlight the importance of these compound effect of climatic and disturbance regime on resilience, consistent with findings from other studies (Batllori et al., 2019; Blanco-Rodríguez et al., 2023; Elvira et al., 2021).

4.1 | *Pinus halepensis*

Our study shows high levels of variability in the resilience of *P. halepensis*, particularly when comparing regions with different climatic conditions such as Catalonia and Murcia, in agreement with previous studies reporting its diverse post-fire performance across its distribution range (Pausas et al., 2004). Recovery rates appear significantly higher in Catalonia, likely due to the moister climatic conditions there (De Las Heras et al., 2008), as opposed to the very low or null recovery in the arid conditions of Murcia.

In Murcia, located at the arid limit of the species' climatic niche (Figure 2), most burned *P. halepensis* forests (77.6%) did not recover well after fire, as indicated by the high net change between pre- and post-fire forests. Although, 37.3% of the sites exhibited recovery towards the EDR, the slow rates of ecosystem response, combined with an expected increase in the frequency of fires in the region, can compromise the future resilience of these forests. This is especially relevant for a seeder species such as *P. halepensis* whose successful regeneration depends on the seed bank stored in the serotinous cones. If severe crown fires occur too frequently, trees may not reach reproductive maturity and may not replenish their seed reserves, ultimately impairing post-fire regeneration (Espelta et al., 2008). Fire severity and pre-fire conditions indicative of populations' marginality

in niche space appear as the most significant factors influencing the lack of resilience in terms of lower recovery and higher net change. Indeed, regardless of the displacement of the ecosystem state induced by fire (i.e. amplitude), populations located far from the dry edge and thus nearer to the climatic optimum (less arid conditions), exhibited better recovery capacity and lower net change.

In Catalonia, the post-fire dynamics of *P. halepensis* forests are more complex. Around 48.7% of burned sites also exhibited changes to shrubland, tree species turnover or low recovery rate (Table 1). This outcome is unexpected in a region where this fire-adapted species is generally assumed to recover well (Fernandes et al., 2008), so we cannot rule out that longer post-disturbance periods could potentially reduce the observed net change values. But, contrary to our expectations, we found that plots closer to the niche edge than to the core (in terms of midterm pre-fire climate) exhibited higher recovery rates under high fire severities. However, such marginal populations exhibiting a high recovery rate in the early post-fire stages are in fact close to the moist edge of the climatic niche—with moister conditions than the niche core—where climate may better support the post-fire recovery of seeding species (Baudena et al., 2020; De Las Heras et al., 2008; Elvira et al., 2021). At low fire severities, however, the recovery rate remains constant regardless of the plots' position within the climatic niche space. Low fire severity can leave structural and biotic remnants, such as the remains of living trees and shrubs, that may impede the recovery of *P. halepensis* due to competition (Sardans et al., 2005). Our results also show that the time span of the climate variability before fire emerges as a relevant factor to understand *P. halepensis* resilience. Lower net change values were found for populations close to the moist edge when considering midterm pre-fire conditions (10 years before the fire) and under high fire severity. By contrast, when considering the immediate pre-fire conditions (3 years before the fire), the net change was higher (i.e. lower resilience) near the moist edge. These results agree with those reported by De las Heras et al. (2008), that observed that along an aridity gradient, populations located in the more humid zones had a greater number of reproductive trees and higher pine cone production, while in drier zones, trees showed higher levels of serotiny and smaller development (i.e. less growth). Therefore, populations historically located in moister areas may have more reproductive individuals and thus higher seed production, although drier conditions shortly before fire could promote cone serotiny, thus enhancing post-fire regeneration through increased seed rain after fire. However, this mechanism may fail under extreme drought conditions before fire, when the seed bank of serotinous cones may be reduced, due to premature cone opening (Espelta et al., 2011) or to lower seed production (Martín-Sanz et al., 2017).

Overall, we observed that net ecosystem change greatly varies depending on the pre- and post-fire climate variability, emphasizing that the sequence of climatic events, that is drought conditions, in relation to fire plays a significant role in Mediterranean ecosystems resilience (Batllori et al., 2019). Whereas the net change was lower when midterm pre-fire conditions were close to the moist climatic niche edge, resilience was also enhanced when post-fire climate (3 years window) was near the niche core (i.e. far from the moist edge). In addition of the supposedly higher adequacy of the core climatic conditions for the species regeneration, this response could also be reinforced by the increased competition that *P. halepensis* likely face from other tree species in more humid areas. Indeed, in spite of the overall resilient performance of burned *P. halepensis* forests in Catalonia, 15.8% of them shifted towards forests dominated by *Quercus* sp. pl. after fire; this occurred especially in plots located near the moist edge of the niche.

Despite the observed significant relationships between *P. halepensis* resilience and climatic conditions in conjunction with fire severity, the low R-square values of the resilience models for Catalonia (amplitude: 0.26; recovery: 0.10; net change: 0.37) indicate that other factors not included in our analysis, such as the interactions with other species (e.g. in the understorey) or post-fire management (Pausas, 2004), may also be important in modulating the post-fire resilience of this species.

4.2 | *Pinus nigra*

In general, we found that *P. nigra* in Catalonia did not recover well after fires, in line with previous studies (Morales-Molino et al., 2017; Ordóñez et al., 2004; Retana et al., 2002). This was especially evident in areas affected by high-severity fires, where *P. nigra* regeneration was rarely successful, whereas its recovery appears enhanced in areas affected by low-intensity fires, predominantly near the climatic niche core (Figure 4, Appendix S1: Figure S7). This also concurs with the ability of this species to survive low-intensity surface fires (Fulé et al., 2008) thanks to the protection provided by its wide bark (Espinosa et al., 2020). In areas where *P. nigra* recovered after fire, it likely faced strong competition from species of the genus *Quercus* (*Q. faginea* and *Q. ilex*, mainly), which tended to dominate the resulting post-fire communities at the time span considered in this study (Table 1; Appendix S1: Figure S5). These ecosystem dynamics highlight the higher competitive ability of resprouting *Quercus* species, such as *Q. faginea*, *Q. pubescens* and the hybrid *Q. subpyrenaica*. over *P. nigra* after fires (Sánchez-Pinillos et al., 2018).

Counterintuitively, we found that topographic exposure, particularly higher dryness levels in more exposed areas (i.e. south facing slopes), relates positively with post-fire recovery and negatively with net change in burned *P. nigra* forests in Catalonia (Figure 4), where water availability is not too low, as reflected by the population's position in the species climatic niche (Figure 2d). These physical drivers associated with water availability likely reflect competitive interactions. Areas with less topographic exposure (i.e. north facing slopes) have more humidity and may be more favourable for the regrowth of *Quercus* sp. pl. trees. The observed dynamics could also be related to the greater shade-intolerance of pines compared with their oak competitors. This pattern is in line with Martín-Alcón and Coll (2016) that observed that post-fire regeneration in *P. nigra* forests was contingent on the topographic aspect: areas facing to the north (less

exposed) were dominated by *Quercus* sp. pl. tree regeneration, while those oriented to the east and west were dominated by *P. nigra*.

In fire-sensitive species such as *P. nigra*, the presence of unburned forest patches after the fire appears key for its regeneration. Although in our study the distance to unburned forest was not significant in the recovery model for this species (Figure 4), it should certainly play a role in forest resilience in fires where no seed sources are left inside the burned area. Indeed, when analysing the significance of each explanatory variable individually (Appendix S1: Table S4), the recovery of this pine appears significantly and negatively related to the distance to unburned areas, from where seeds arrive (Christopoulou et al., 2014; Martín-Alcón & Coll, 2016).

Overall, although longer recovery periods are necessary to definitely determine forest resilience to fires, our results showed the difficulties that areas burned at high fire severities have to become forests dominated by *P. nigra* again (Morales-Molino et al., 2017). Therefore, forests dominated by this pine species could confront a more critical situation than other Mediterranean forests, especially under the contemporary context of frequent, extreme fires (Duane et al., 2021).

5 | CONCLUSION

Our analysis exposes factors related to post-fire resilience in Mediterranean pines with different fire adaptations. Specifically, this study contributes to a better understanding of the effect of climate variability on post-fire resilience in the Mediterranean forests of *Pinus halepensis* and *Pinus nigra* in the Iberian Peninsula, based on a new vision that integrates the concepts of EDRs and the temporal characterization of the species climate niche. Our approach demonstrates that the climatic conditions both before and after fire are key to understanding forest resilience under a dynamic ecological perspective. The centrality–marginality effect in the climatic niche space partially explains variations in fire resilience: higher resilience near the core and lower resilience, especially at the dry edge of the climatic niche. As such, the climatic characterization of the edge of species' climatic niches emerges as a critical factor to understand the influence of pre- and post-fire climate variability. We also underline the relevance of the biology and ecology of each species to interpret their resilience, as in the case of *P. halepensis*, a seeder species adapted to fire, and *P. nigra*, a species sensitive to crown fire. Overall, we uncover how climate change (translated into climatic marginality in niche space) and the increase in fire severity can jeopardize the future of Mediterranean pine forests.

AUTHOR CONTRIBUTIONS

Gerard Codina, contributed to the conceptualization, planning and development of the methodology; performed the analyses; contributed to the interpretation of results; and participated in the writing and revision of the manuscript. Martina Sánchez-Pinillos conceived and planned the assessment of ecological resilience using ecological dynamic regimes; contributed to interpreting the results; and participated in writing and revising the manuscript. Francisco Lloret supervised the study; contributed to the conceptualization, planning and development of the methodology; contributed to interpreting the results; and participated in writing and revising the manuscript. Judit Lecina-Diaz provided fire data and fire-severity calculations, and revised the manuscript. Enric Batllori supervised the study; contributed to the conceptualization, planning and development of the methodology; contributed to interpreting the results; and participated in writing and revising the manuscript.

ACKNOWLEDGEMENTS

Gerard Codina, Enric Batllori and Francisco Lloret received funding from Ministerio Ciencia y Innovación, Spanish Government (grant PID2020-115264RB-I00) and AGAUR, Generalitat de Catalunya (grant 2021-SGR 00849). Gerard Codina received funding from the grant Beca Impulsa CREAF-Barraquer. Martina Sánchez-Pinillos received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 891477 (RESET project) and an NSERC Alliance—Mitacs Accelerate grant (DIVERSE project). Enric Batllori is a Serra Húnter fellow.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest related to this manuscript.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70261.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from publicly accessible sources. Forest structure and composition data were obtained from the Spanish National Forest Inventory (IFN2, IFN3 and IFN4, 1986–2016) and are available through the Ministerio para la Transición Ecológica y el Reto Demográfico at https://www.miteco.gob.es/ca/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html. Geographic distribution and occurrence data for tree species were sourced from EUForest (Mauri et al., 2017) at https://figshare.com/collections/A_high-resolution_pan-European_tree_occurrence_dataset/3288407. Fire severity data were derived from Landsat-based products available through the Google Earth Engine platform, using relativized differenced Normalized Burn Ratio (RdNBR) metrics, as described in Alvarez et al. (2024). Bioclimatic variables were obtained from the CHELSA data base at https://www.chelsa-climate.org/datasets. All processed datasets used in the analyses, together with the R scripts required to calculate resilience indices and to characterize climatic niche cores and edges, are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.np5hqc085; Codina et al., 2025).

ORCID

Gerard Codina https://orcid.org/0009-0009-3753-9361
Francisco Lloret https://orcid.org/0000-0002-9836-4069

REFERENCES

Abbott, K. C., Cuddington, K., & Hastings, A. (2021). Transients in ecology: Stochasticity, management, and understanding. *Theoretical Ecology*, *14*, 623–624. https://doi.org/10.1007/s12080-021-00524-8

Alvarez, A., Lecina-Diaz, J., Batllori, E., Duane, A., Brotons, L., & Retana, J. (2024). Spatiotemporal patterns and drivers of extreme fire severity in Spain for the period 1985–2018. *Agricultural and Forest Meteorology*, *358*, 110185. https://doi.org/10.1016/j.agrformet.2024.110185

Batllori, E., De Cáceres, M., Brotons, L., Ackerly, D. D., Moritz, M. A., & Lloret, F. (2019). Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems. *Journal of Ecology*, *107*, 1187–1198. https://doi.org/10.1111/1365-2745.13115

Baudena, M., Santana, V. M., Baeza, M. J., Bautista, S., Eppinga, M. B., Hemerik, L., Garcia Mayor, A., Rodriguez, F., Valdecantos, A., Vallejo, V. R., Vasques, A., & Rietkerk, M. (2020). Increased aridity drives post-fire recovery of Mediterranean forests towards open shrublands. *The New Phytologist*, *225*, 1500–1515. https://doi.org/10.1111/nph.16252

Besnard, S., Carvalhais, N., Arain, M. A., Black, A., Brede, B., Buchmann, N., Chen, J., Clevers, J. G. P. W., Dutrieux, L. P., Gans, F., Herold, M., Jung, M., Kosugi, Y., Knohl, A., Law, B. E., Paul-Limoges, E., Lohila, A., Merbold, L., Roupsard, O., … Reichstein, M. (2019). Memory effects of climate and vegetation affecting net ecosystem CO_2 fluxes in global forests. *PLoS One*, *14*, e0211510. https://doi.org/10.1371/journal.pone.0211510

Blanco-Rodríguez, M. Á., Ameztegui, A., Gelabert, P., Rodrigues, M., & Coll, L. (2023). Short-term recovery of post-fire vegetation is primarily limited by drought in Mediterranean forest ecosystems. *Fire Ecology*, *19*, 68. https://doi.org/10.1186/s42408-023-00228-w

Bond, W. J., & Keeley, J. E. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*, 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Botella-Martínez, M. A., & Fernández-Manso, A. (2017). Estudio de la severidad post-incendio en la Comunidad Valenciana comparando los índices dNBR, RdNBR y RBR a partir de imágenes Landsat 8. *Revista de Teledeteccion*, *2017*, 33. https://doi.org/10.4995/raet.2017.7095

Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H., & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, *21*, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Broncano, M. J., Rodrigo, A., & Retana, J. (2008). Post-dispersal seed predation in *Pinus halepensis* and consequences on seedling establishment after fire. *International Journal of Wildland Fire*, *17*, 407–414. https://doi.org/10.1071/WF07095

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, *124*, 255–279. https://doi.org/10.1086/284267

Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L., & Karger, D. N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*, *14*, 5573–5603. https://doi.org/10.5194/essd-14-5573-2022

Calheiros, T., Pereira, M. G., & Nunes, J. P. (2021). Assessing impacts of future climate change on extreme fire weather and pyro-regions in Iberian Peninsula. *Science of the Total Environment*, *754*, 142233. https://doi.org/10.1016/j.scitotenv.2020.142233

Camarero, J. J., Manzanedo, R. D., Sanchez-Salguero, R., & Navarro-Cerrillo, R. M. (2013). Growth response to climate and drought change along an aridity gradient in the southernmost *Pinus nigra* relict forests. *Annals of Forest Science*, *70*, 769–780. https://doi.org/10.1007/s13595-013-0321-9

Chacón, J. E., & Duong, T. (2018). *Multivariate Kernel smoothing and its applications*. Chapman and Hall/CRC. https://doi.org/10.1201/9780429485572

Christopoulou, A., Fyllas, N. M., Andriopoulos, P., Koutsias, N., Dimitrakopoulos, P. G., & Arianoutsou, M. (2014). Post-fire regeneration patterns of *Pinus nigra* in a recently burned area in Mount Taygetos, southern Greece: The role of unburned forest patches. *Forest Ecology and Management*, *327*, 148–156. https://doi.org/10.1016/j.foreco.2014.05.006

Codina, G., Sánchez-Pinillos, M., Lloret, F., Lecina-Diaz, J., & Batllori, E. (2025). Climatic niche position determines post-fire resilience in Mediterranean forests [dataset]. *Dryad*. https://doi.org/10.5061/dryad.np5hqc085

Coop, J. D., Parks, S. A., Stevens-Rumann, C. S., Crausbay, S. D., Higuera, P. E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B. M., Davis, K. T., Dobrowski, S., Falk, D. A., Fornwalt, P. J., Fulé, P. Z., Harvey, B. J., Kane, V. R., Littlefield, C. E., Margolis, E. Q., … Rodman, K. C. (2020). Wildfire-driven Forest conversion in Western North American landscapes. *Bioscience*, *70*, 659–673. https://doi.org/10.1093/biosci/biaa061

Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., Welk, E., Stott, I., Enquist, B. J., McGill, B., Svenning, J.-C., Violle, C., & Buckley, Y. M. (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, *20*, 969–980. https://doi.org/10.1111/ele.12794

Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., Parks, S. A., Sala, A., & Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences*, *116*, 6193–6198. https://doi.org/10.1073/pnas.1815107116

De Cáceres, M. (2012). vegclust: Fuzzy Clustering of Vegetation Data. https://doi.org/10.32614/CRAN.package.vegclust

De Cáceres, M., Legendre, P., & He, F. (2013). Dissimilarity measurements and the size structure of ecological communities. *Methods in Ecology and Evolution*, *4*, 1167–1177. https://doi.org/10.1111/2041-210X.12116

De las Heras, J., Martínez-Sánchez, J. J., González-Ochoa, A. I., Ferrandis, P., & Herranz, J. M. (2002). Establishment of *Pinus halepensis* Mill. Saplings following fire: Effects of competition with shrub species. *Acta Oecologica*, *23*, 91–97. https://doi.org/10.1016/S1146-609X(02)01138-4

De Las Heras, J., Moya, D., López-Serrano, F. R., Eugenio, M., & Espelta, J. M. (2008). *Aleppo pine regeneration after fire along an aridity gradient*. Presented at the FOREST FIRES 2008, Toledo, Spain, pp. 289–295 https://doi.org/10.2495/FIVA080291

Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, *467*, 959–962. https://doi.org/10.1038/nature09439

Duane, A., Castellnou, M., & Brotons, L. (2021). Towards a comprehensive look at global drivers of novel extreme wildfire events. *Climatic Change*, *165*, 43. https://doi.org/10.1007/s10584-021-03066-4

Elvira, N. J., Lloret, F., Jaime, L., Margalef-Marrase, J., Pérez Navarro, M. Á., & Batllori, E. (2021). Species climatic niche explains post-fire regeneration of Aleppo pine (*Pinus halepensis* Mill.) under compounded effects of fire and drought in east Spain. *Science of the Total Environment*, *798*, 149308. https://doi.org/10.1016/j.scitotenv.2021.149308

Elvira, N. J., Lloret, F., Margalef-Marrase, J., Díaz Borrego, R., & Batllori, E. (2025). Position in the climatic niche modulates post-fire performance of *Pinus halepensis* regeneration. *Forest Ecology and Management*, *580*, 122516. https://doi.org/10.1016/j.foreco.2025.122516

Espelta, J. M., Arnan, X., & Rodrigo, A. (2011). Non-fire induced seed release ina weakly serotinous pine: Climatic factors, maintenance costs or both? *Oikos*, *120*, 1752–1760. https://doi.org/10.1111/j.1600-0706.2011.19570.x

Espelta, J. M., Verkaik, I., Eugenio, M., & Lloret, F. (2008). Recurrent wildfires constrain long-term reproduction ability in Pinus halepensis Mill. *International Journal of Wildland Fire*, *17*, 579–585. https://doi.org/10.1071/WF07078

Espinosa, J., Rodríguez de Rivera, O., Madrigal, J., Guijarro, M., & Hernando, C. (2020). Predicting potential cambium damage and fire resistance in *Pinus nigra* Arn. ssp. *salzmannii*. *Forest Ecology and Management*, *474*, 118372. https://doi.org/10.1016/j.foreco.2020.118372

Fernandes, P. M., Vega, J. A., Jiménez, E., & Rigolot, E. (2008). Fire resistance of European pines. *Forest Ecology and Management*, *256*, 246–255. https://doi.org/10.1016/j.foreco.2008.04.032

Fernández-García, V., Fulé, P. Z., Marcos, E., & Calvo, L. (2019). The role of fire frequency and severity on the regeneration of Mediterranean serotinous pines under different environmental conditions. *Forest Ecology and Management*, *444*, 59–68. https://doi.org/10.1016/j.foreco.2019.04.040

Fernández-García, V., Marcos, E., Reyes, O., & Calvo, L. (2020). Do fire regime attributes affect soil biochemical properties in the same way under different environmental conditions? *Forests*, *11*, 274. https://doi.org/10.3390/f11030274

Fulé, P. Z., Ribas, M., Gutiérrez, E., Vallejo, R., & Kaye, M. W. (2008). Forest structure and fire history in an old *Pinus nigra* forest, eastern Spain. *Forest Ecology and Management*, *255*, 1234–1242. https://doi.org/10.1016/j.foreco.2007.10.046

Gil-Tena, A., Aquilué, N., Duane, A., De Cáceres, M., & Brotons, L. (2016). Mediterranean fire regime effects on pine-oak forest landscape mosaics under global change in NE Spain. *European Journal of Forest Research*, *135*, 403–416. https://doi.org/10.1007/s10342-016-0943-1

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., & Zavala, M. A. (2011). Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Global Change Biology*, *17*, 2400–2414. https://doi.org/10.1111/j.1365-2486.2011.02421.x

González-De Vega, S., De las Heras, J., & Moya, D. (2018). Post-fire regeneration and diversity response to burn severity in *Pinus halepensis* Mill. forests. *Forests*, *9*, 299. https://doi.org/10.3390/f9060299

Grau-Andrés, R., Moreira, B., & Pausas, J. G. (2024). Global plant responses to intensified fire regimes. *Global Ecology and Biogeography*, *33*, e13858. https://doi.org/10.1111/geb.13858

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, *52*, 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hao, B., Xu, X., Wu, F., & Tan, L. (2022). Long-term effects of fire severity and climatic factors on post-Forest-fire vegetation recovery. *Forests*, *13*, 883. https://doi.org/10.3390/f13060883

Hartig, F., & Hartig, M. F. (2022). Package "dharma". R Package. https://CRAN.R-project.org/package=DHARMa

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*, 1983–2010. https://doi.org/10.1111/brv.12544

Hiers, J. K., Mitchell, R. J., Barnett, A., Walters, J. R., Mack, M., Williams, B., & Sutter, R. (2012). The dynamic reference concept: Measuring restoration success in a rapidly changing no-analogue future. *Ecological Restoration*, *30*, 27–36. https://doi.org/10.3368/er.30.1.27

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology, Evolution, and Systematics*, *4*, 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. https://doi.org/10.1101/sqb.1957.022.01.039

Jaime, L., Batllori, E., Ferretti, M., & Lloret, F. (2022). Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests. *Global Change Biology*, *28*, 2830–2841. https://doi.org/10.1111/gcb.16106

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*, 369–378. https://doi.org/10.1002/fee.1311

Karavani, A., Boer, M. M., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J., de Luis, M., Enríquez-de-Salamanca, Á., & Resco de Dios, V. (2018). Fire-induced deforestation in drought-prone Mediterranean forests: Drivers and unknowns from leaves to communities. *Ecological Monographs*, *88*, 141–169. https://doi.org/10.1002/ecm.1285

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122. https://doi.org/10.1038/sdata.2017.122

Kaufman, L., & Rousseeuw, P. (1990). Partition Around Medoids (Program Pam) 68.

Keeley, J. E., & Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics*, *53*, 203–225. https://doi.org/10.1146/annurev-ecolsys-102320-095612

Kelly, L. T., Giljohann, K. M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A. F., Buckland, S. T., Canelles, Q., Clarke, M. F., Fortin, M.-J., Hermoso, V., Herrando, S., Keane, R. E., Lake, F. K., McCarthy, M. A., Morán-Ordóñez, A., Parr, C. L., Pausas, J. G., … Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science*, *370*, eabb0355. https://doi.org/10.1126/science.abb0355

Le Breton, T. D., Lyons, M. B., Nolan, R. H., Penman, T., Williamson, G. J., & Ooi, M. K. (2022). Megafire-induced interval squeeze threatens vegetation at landscape scales. *Frontiers in Ecology and the Environment*, *20*, 327–334. https://doi.org/10.1002/fee.2482

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, *120*, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x

Lloret, F., Martinez-Vilalta, J., Serra-Diaz, J. M., & Ninyerola, M. (2013). Relationship between projected changes in future climatic suitability and demographic and functional traits of forest tree species in Spain. *Climatic Change*, *120*, 449–462. https://doi.org/10.1007/s10584-013-0820-6

Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., & Fagan, W. F. (2014). How climate extremes—Not means—Define a species' geographic range boundary via a demographic tipping point. *Ecological Monographs*, *84*, 131–149. https://doi.org/10.1890/12-2235.1

Maguire, B. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist*, *107*(954), 213–246. https://doi.org/10.1086/282827

Margalef-Marrase, J., Pérez-Navarro, M. Á., & Lloret, F. (2020). Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species. *Global Change Biology*, *26*, 3134–3146. https://doi.org/10.1111/gcb.15042

Martín-Alcón, S., & Coll, L. (2016). Unraveling the relative importance of factors driving post-fire regeneration trajectories in non-serotinous *Pinus nigra* forests. *Forest Ecology and Management*, *361*, 13–22. https://doi.org/10.1016/j.foreco.2015.11.006

Martín-Sanz, R. C., Callejas-Díaz, M., Tonnabel, J., & Climent, J. M. (2017). Maintenance costs of serotiny in a variably serotinous pine:

The role of water supply. *PLoS One*, *12*, e0181648. https://doi.org/10.1371/journal.pone.0181648

Mauri, A., Strona, G., & San-Miguel-Ayanz, J. (2017). EU-Forest, a high-resolution tree ocurrence dataset for Europe. *Scientific Data*, *4*, 1–8. https://figshare.com/collections/A_high-resolution_pan-European_tree_occurrence_dataset/3288407

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., Tepley, A. J., Varner, J. M., Veblen, T. T., Adalsteinsson, S. A., Balch, J. K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M. L., Coen, J., Crandall, R., … Watts, A. C. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology*, *108*, 2047–2069. https://doi.org/10.1111/1365-2745.13403

Mendez-Cartin, A. L., Coll, L., Valor, T., Torné-Solà, G., & Ameztegui, A. (2024). Post-fire growth of *Pinus halepensis*: Shifts in the mode of competition along a precipitation gradient. *Forest Ecology and Management*, *554*, 121693. https://doi.org/10.1016/j.foreco.2024.121693

Miller, J. D., & Thode, A. E. (2007). Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment*, *109*, 66–80. https://doi.org/10.1016/j.rse.2006.12.006

Ministerio de Medio Ambiente. (1995). Segundo Inventario Forestal Nacional (1986–1995). Madrid, Spain.

Ministerio de Medio Ambiente. (2007). Tercer Inventario Forestal Nacional (1997–2007). Madrid, Spain.

Ministerio para la Transición Ecológica y el Reto Demográfico. (2012). Cuarto Inventario Forestal Nacional - Murcia. Madrid, Spain.

Ministerio para la Transición Ecológica y el Reto Demográfico. (2017). Cuarto Inventario Forestal Nacional - Cataluña. Madrid, Spain.

Ministerio para la Transición Ecológica y el Reto Demográfico. (2024). Cuarto Inventario Forestal Nacional (2008–2023). Madrid, Spain.

Morales-Molino, C., Tinner, W., García-Antón, M., & Colombaroli, D. (2017). The historical demise of *Pinus nigra* forests in the northern Iberian Plateau (south-western Europe). *Journal of Ecology*, *105*, 634–646. https://doi.org/10.1111/1365-2745.12702

Moss, W. E., Crausbay, S. D., Rangwala, I., Wason, J. W., Trauernicht, C., Stevens-Rumann, C. S., Sala, A., Rottler, C. M., Pederson, G. T., Miller, B. W., Magness, D. R., Littell, J. S., Frelich, L. E., Frazier, A. G., Davis, K. T., Coop, J. D., Cartwright, J. M., & Booth, R. K. (2024). Drought as an emergent driver of ecological transformation in the twenty-first century. *Bioscience*, *74*, 524–538. https://doi.org/10.1093/biosci/biae050

Navarro-Cerrillo, R. M., Duque-Lazo, J., Manzanedo, R. D., Sánchez-Salguero, R., & Palacios-Rodriguez, G. (2018). Climate change may threaten the southernmost *Pinus nigra* subsp. *salzmannii* (Dunal) Franco populations: An ensemble niche-based approach. *iForest - Biogeosciences and Forestry*, *11*, 396–405.

Naveh, Z. (1975). The evolutionary significance of fire in the mediterranean region. *Vegetatio*, *29*, 199–208. https://doi.org/10.1007/BF02390011

Ne'eman, G., Goubitz, S., & Nathan, R. (2004). Reproductive traits of Pinus halepensis in the light of fire—A critical review. *Plant Ecology*, *171*, 69–79. https://doi.org/10.1023/B:VEGE.0000029380.04821.99

Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., Resco de Dios, V., & Bradstock, R. (2021). Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment*, *44*, 3471–3489. https://doi.org/10.1111/pce.14176

Ooi, M. K. J., Denham, A. J., Santana, V. M., & Auld, T. D. (2014). Temperature thresholds of physically dormant seeds and plant functional response to fire: Variation among species and relative impact of climate change. *Ecology and Evolution*, *4*, 656–671. https://doi.org/10.1002/ece3.973

Ordóñez, J. L., Franco, S., & Retana, J. (2004). Limitation of the recruitment of *Pinus nigra* in a gradient of post-fire environmental conditions1. *Écoscience*, *11*, 296–304. https://doi.org/10.1080/11956860.2004.11682836

Ordoñez-Salanueva, C. A., Orozco-Segovia, A., Mattana, E., Castillo-Lorenzo, E., Davila-Aranda, P., Pritchard, H. W., Ulian, T., & Flores-Ortiz, C. M. (2021). Thermal niche for germination and early seedling establishment at the leading edge of two pine species, under a changing climate. *Environmental and Experimental Botany*, *181*, 104288. https://doi.org/10.1016/j.envexpbot.2020.104288

Pachauri, R. K., Mayer, L., & Intergovernmental Panel on Climate Change. (2015). *Climate change 2014: Synthesis report*. Intergovernmental Panel on Climate Change.

Parks, S. A., & Abatzoglou, J. T. (2020). Warmer and drier fire seasons contribute to increases in area burned at high severity in Western US forests from 1985 to 2017. *Geophysical Research Letters*, *47*, e2020GL089858. https://doi.org/10.1029/2020GL089858

Parks, S. A., Dillon, G. K., & Miller, C. (2014). A new metric for quantifying burn severity: The relativized burn ratio. *Remote Sensing*, *6*, 1827–1844. https://doi.org/10.3390/rs6031827

Parks, S. A., Holsinger, L. M., Voss, M. A., Loehman, R. A., & Robinson, N. P. (2018). Mean composite fire severity metrics computed with Google earth engine offer improved accuracy and expanded mapping potential. *Remote Sensing*, *10*, 879. https://doi.org/10.3390/rs10060879

Pausas, J. G. (2004). Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean Basin). *Climatic Change*, *63*(3), 337–350. https://doi.org/10.1023/b:clim.0000018508.94901.9c

Pausas, J. G., & Keeley, J. E. (2019). Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment*, *17*, 289–295. https://doi.org/10.1002/fee.2044

Pausas, J. G., Llovet, J., Rodrigo, A., & Vallejo, R. (2008). Are wildfires a disaster in the Mediterranean basin?—A review. *International Journal of Wildland Fire*, *17*, 713–723. https://doi.org/10.1071/WF07151

Pausas, J. G., Ouadah, N., Ferran, A., Gimeno, T., & Vallejo, R. (2002). Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. *Plant Ecology*, *169*, 205–213. https://doi.org/10.1023/A:1026019528443

Pausas, J. G., Ribeiro, E., & Vallejo, R. (2004). Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *Forest Ecology and Management*, *203*, 251–259. https://doi.org/10.1016/j.foreco.2004.07.061

Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Bagaria, G., Guisan, A., & Lloret, F. (2022). Comparing climatic suitability and niche distances to explain populations responses to extreme climatic events. *Ecography*, *2022*, e06263. https://doi.org/10.1111/ecog.06263

Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Moya-Perez, J. M., Carreño, M. F., Guisan, A., & Lloret, F. (2021). Temporal variability is key to modelling the climatic niche. *Diversity and Distributions*, *27*, 473–484. https://doi.org/10.1111/ddi.13207

Perez-Navarro, M. A., Lloret, F., Molina-Venegas, R., Alcántara, J. M., & Verdú, M. (2024). Plant canopies promote climatic disequilibrium in Mediterranean recruit communities. *Ecology Letters*, *27*, e14391. https://doi.org/10.1111/ele.14391

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Retana, J., Maria Espelta, J., Habrouk, A., Luis OrdoÑEz, J., & de Solà-Morales, F. (2002). Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience*, *9*, 89–97. https://doi.org/10.1080/11956860.2002.11682694

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T. E., & Rivas-Sáenz, S. (2017). Bioclimatology of the Iberian Peninsula and the Balearic Islands. *The Vegetation of the Iberian Peninsula*, *29–80*. https://doi.org/10.1007/978-3-319-54784-8_2

Sánchez-Pinillos, M., Ameztegui, A., Kitzberger, T., & Coll, L. (2018). Relative size to resprouters determines post-fire recruitment of non-serotinous pines. *Forest Ecology and Management*, *429*, 300–307. https://doi.org/10.1016/j.foreco.2018.07.009

Sánchez-Pinillos, M., Dakos, V., & Kéfi, S. (2024). Ecological dynamic regimes: A key concept for assessing ecological resilience. *Biological Conservation*, *289*, 110409. https://doi.org/10.1016/j.biocon.2023.110409

Sánchez-Pinillos, M., De Cáceres, M., Casals, P., Alvarez, A., Beltrán, M., Pausas, J. G., Vayreda, J., & Coll, L. (2021). Spatial and temporal variations of overstory and understory fuels in Mediterranean landscapes. *Forest Ecology and Management*, *490*, 119094. https://doi.org/10.1016/j.foreco.2021.119094

Sánchez-Pinillos, M., Kéfi, S., De Cáceres, M., & Dakos, V. (2023). Ecological dynamic regimes: Identification, characterization, and comparison. *Ecological Monographs*, *93*, e1589. https://doi.org/10.1002/ecm.1589

Sánchez-Pinillos, M., Leduc, A., Ameztegui, A., Kneeshaw, D., Lloret, F., & Coll, L. (2019). Resistance, resilience or change: Post-disturbance dynamics of boreal forests after insect outbreaks. *Ecosystems*, *22*, 1886–1901. https://doi.org/10.1007/s10021-019-00378-6

Sardans, J., Peñuelas, J., & Rodà, F. (2005). Changes in nutrient use efficiency, status and retranslocation in young post-fire regeneration *Pinus halepensis* in response to sudden N and P input, irrigation and removal of competing vegetation. *Trees*, *19*, 233–250. https://doi.org/10.1007/s00468-004-0374-3

Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L., & Hicke, J. A. (2016). REVIEW: Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology*, *53*, 120–129. https://doi.org/10.1111/1365-2664.12511

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Turco, M., Rosa-Cánovas, J. J., Bedia, J., Jerez, S., Montávez, J. P., Llasat, M. C., & Provenzale, A. (2018). Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate-fire models. *Nature Communications*, *9*, 3821. https://doi.org/10.1038/s41467-018-06358-z

Turner, M. G., & Seidl, R. (2023). Novel disturbance regimes and ecological responses. *Annual Review of Ecology, Evolution, and Systematics*, *54*, 63–83. https://doi.org/10.1146/annurev-ecolsys-110421-101120

Viana-Soto, A., Aguado, I., & Martínez, S. (2017). Assessment of post-fire vegetation recovery using fire severity and geographical data in the Mediterranean region (Spain). *Environments*, *4*, 90. https://doi.org/10.3390/environments4040090

Xu, Z., Johnson, D. J., Zhu, K., Lin, F., Ye, J., Yuan, Z., Mao, Z., Fang, S., Hao, Z., & Wang, X. (2022). Interannual climate variability has predominant effects on seedling survival in a temperate forest. *Ecology*, *103*, e3643. https://doi.org/10.1002/ecy.3643

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species observed in the studied forests, sorted by their relative abundance.

Table S2. Comparison of AIC and marginal and conditional R^2 values (R^2_m and R^2_c, respectively) for models selected using the stepwise method for *Pinus halepensis* in Murcia. The values corresponding to the final selected model are highlighted in bold.

Table S3. Comparison of AIC and marginal and conditional R^2 values (R^2_m and R^2_c, respectively) for models selected using the stepwise method for *Pinus halepensis* in Catalonia. The values corresponding to the final selected model are highlighted in bold.

Table S4. Comparison of AIC and marginal and conditional R^2 values (R^2_m and R^2_c, respectively) for models selected using the stepwise method for *Pinus nigra* in Catalonia. The values corresponding to the final selected model are highlighted in bold.

Table S5. Results of multivariant linear mixed model for resilience metric of amplitude for *Pinus halepensis* in Murcia.

Table S6. Results of multivariant linear mixed model for resilience metric of recovery for *Pinus halepensis* in Murcia.

Table S7. Results of multivariant linear mixed model for resilience metric of net change for *Pinus halepensis* in Murcia.

Table S8. Results of multivariant linear mixed model for resilience metric of amplitude for *Pinus halepensis* in Catalonia.

Table S9. Results of multivariant linear mixed model for resilience metric of recovery for *Pinus halepensis* in Catalonia.

Table S10. Results of multivariant linear mixed model for resilience metric of net change for *Pinus halepensis* in Catalonia.

Table S11. Results of multivariant linear mixed model for resilience metric of amplitude for *Pinus nigra* in Catalonia.

Table S12. Results of multivariant linear mixed model for resilience metric of recovery for *Pinus nigra* in Catalonia.

Table S13. Results of multivariant linear mixed model for resilience metric of net change for *Pinus nigra* in Catalonia.

Table S14. Results of univariant linear mixed model for resilience metrics of amplitude (A), recovery (R) and net change (NC) for *Pinus halepensis* in Murcia.

Table S15. Results of univariant linear mixed model for resilience metrics of amplitude (A), recovery (R) and net change (NC) for *Pinus halepensis* in Catalonia.

Table S16. Results of univariant linear mixed model for resilience metrics of amplitude (A), recovery (R) and net change (NC) for *Pinus nigra* in Catalonia.

Figure S1. Correlation circle obtained from PCA from the fifteen selected climate variables. Where bio1 (mean annual air temperature), bio4 (temperature seasonality), bio5 (mean daily maximum air temperature of the warmest month), bio6 (mean daily minimum air temperature of the coldest month), bio10 (mean daily mean air temperatures of the warmest quarter), bio11 (mean daily mean air temperatures of the coldest quarter), bio12 (annual precipitation amount), bio13 (precipitation amount of the wettest month), bio14 (precipitation amount of the driest month), bio15 (precipitation seasonality), bio16 (mean monthly precipitation amount of the wettest quarter), bio17 (mean monthly precipitation amount of the driest quarter), bio18 (mean monthly precipitation amount of the warmest quarter), PET (potential evapotranspiration), and VPD (vapour pressure deficit).

Figure S2. Climatic niche edges for *Pinus halepensis* within the two-dimensional PCA-derived climatic space. The centroid of the species' climatic niche (intersection of dashed lines) was used to define four quadrants corresponding to distinct climatic conditions. Based on the distribution of precipitation and temperature along both axes, the upper-left and lower-right quadrants were identified as moist

and dry regions, respectively. Within these, the niche edges were defined as the 5% lowest occurrence density values, representing the dry edge (orange) and the moist edge (blue). Grey points indicate intermediate conditions.

Figure S3. Figure S2. Climatic niche edges for *Pinus nigra* within the two-dimensional PCA-derived climatic space. The centroid of the species' climatic niche (intersection of dashed lines) was used to define four quadrants corresponding to distinct climatic conditions. Based on the distribution of precipitation and temperature along both axes, the upper-left and lower-right quadrants were identified as moist and dry regions, respectively. Within these, the niche edges were defined as the 5% lowest occurrence density values, representing the dry edge (orange) and the moist edge (blue). Grey points indicate intermediate conditions.

Figure S4. Forests types included in EDRs for each region.

Figure S5. Ecological dynamical regime (EDR) based on the representative trajectory (blue) and burned trajectories (red) of *Pinus halepensis* forests in Murcia. In grey, the successional trajectories of non-disturbed forests of *P. halepensis*, from which the representative trajectory is calculated (above). Forest type between states along the successional trajectories. Blueish dots represent pine forests and brownish dots represents oak forests (below).

Figure S6. Ecological dynamical regime (EDR) based on the representative trajectory (blue) and burned trajectories (red) of *Pinus halepensis* forests in Catalonia. In grey, the successional trajectories of non-disturbed forests of *P. halepensis*, from which the representative trajectory is calculated (top panel). Forest type between states along the successional trajectories. Blueish dots represent pine forests and brownish dots represent oak forests (bottom panel). See Figure S2 for species names and distribution in the study areas.

Figure S7. Ecological dynamical regime (EDR) based on the representative trajectory (blue) and burned trajectories (red) of *Pinus nigra* forests in Catalonia. In grey, the successional trajectories of non-disturbed forests of P. nigra, from which the representative trajectory is calculated (top panel). Forest type between states along the successional trajectories. Blueish dots represent pine forests and brownish dots represent oak forests (bottom panel). See Figure S2 for species names and distribution in the study areas.

Figure S8. Effect of the interaction between fire severity (Severity) and climatic niche distance to the edge midterm pre-fire (DE10_pre) in relation to amplitude in forests dominated by *Pinus halepensis* in Murcia.

Figure S9. Effect of the interaction between fire severity (Severity) and climatic niche distance to the edge midterm pre-fire (DE10_pre) in relation to amplitude and recovery in forests dominated by *Pinus nigra* in Catalonia.

Figure S10. Effect of the interaction between fire severity (Severity) and climatic niche distance to the edge immediate pre-fire (DE3_pre) and immediate post-fire (DE3_post) in relation to net change in forests dominated by *Pinus halepensis* in Catalonia.

Figure S11. Comparison of the values of resilience indices (amplitude, recovery, and net change) between *Pinus halepensis* forests located on the dry or moist edges of the climatic niche in three different periods (10 years before fire, 3 years before fire and 3 years after fire). Boxes' lower and upper hinges show the 25%–75% percentile range, and boxes' horizontal lines correspond to median value for each resilience metric. Differences between dry and moist edge plots were tested using the Wilcoxon rank-sum test, and are considered significant when $p < 0.05$.

Figure S12. Comparison of the values of resilience indices (amplitude, recovery, and net change) between *Pinus nigra* forests located on the dry or moist edges of the climatic niche in two different periods (3 years before fire and 3 years after fire). Boxes' lower and upper hinges show the 25%–75% percentile range, and boxes' horizontal lines correspond to median value for each resilience metric. Differences between dry- and moist-edge plots were tested using the Wilcoxon rank-sum test, and are considered significant when $p < 0.05$.

How to cite this article: Codina, G., Sánchez-Pinillos, M., Lloret, F., Lecina-Diaz, J., & Batllori, E. (2026). Climatic niche position determines post-fire resilience in Mediterranean forests. *Journal of Ecology*, *114*, e70261. https://doi.org/10.1111/1365-2745.70261